STUDIES ON JUVENILITY OF MANGOSTEEN

(*GARCINIA MANGOSTANA* L.)

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF THE UNIVERSITY OF HAWAI'I IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

IN

HORTICULTURE

AUGUST 2000

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ACKNOWLEDGEMENTS

I would like to express my sincere gratitude to Dr. M.A. Nagao, chairperson and all dissertation committee, namely Dr. D.P. Bartholomew, Dr. H.C. Bittenbender, Dr. C.L. Chia, Dr. R.A. Criley, and Dr. B. Sakai for the enthusiastic supervision, advice, and constructive criticism as well as English improvement.

Many thanks to the staff of Chanthaburi Horticultural Research Center, Department of Agriculture, Royal Thai government, for their assistance during my experiment in Thailand.

Also, I wish to acknowledge the staff of Department of Tropical Plant and Soil Science, College of Tropical Agriculture and Human Resources, University of Hawai'i at Manoa for their assistance during my study in the United States of America.

Certainly, my family and my friends for their encouragement at all time.

ABSTRACT

A study of juvenility in mangosteen (*Garcinia mangostana* L.) trees was undertaken in Thailand between 1995 and 1998. It was found that the growth rates of trees at the juvenile, near mature and mature phases were significantly different and could be used to distinguish the phase change of mangosteen. Tree age and canopy size were also characteristics associated with maturation, and that canopy size was more highly correlated with phase change than age. The phase change in mangosteen was associated with and possibly determined by the attainment of a minimum canopy size.

Maximal photosynthetic rate ($P_{n\,(max)}$) was 8.52 μmol m^{-2} s^{-1} and light above 600 μmol m^{-2} s^{-1} of PPFD saturated the photosynthetic response of leaves exposed to full sun. Quantum efficiency was 0.03 mol mol^{-1}. Leaves growing inside the canopy had increased size, dry weight and specific leaf area (decreased leaf thickness), and lower P_n rate than leaves exposed to full sun on the same tree. The stomatal conductance (g_s) at PPFD saturation point was about 390 mmol m^{-2} s^{-1}.

The growth regulators, GA_{4+7}, BA, GA_{4+7} + BA, and thiourea + dextrose and photoperiod extension treatments significantly accelerated growth of young mangosteen plants under nursery conditions and resulted in taller plants with greater total leaf area when compared to the untreated controls. Thiourea + dextrose and 2-hour-photoperiod extension treatments resulted in more growth than did other growth regulator and photoperiod treatments. After field transplanting, all treated trees increased their canopy size more rapidly than the untreated trees. With this accelerated rate of development, the

treated trees might be able to attain the minimum size associated with maturation earlier than the controls.

Water stress and appropriate water management strategies after attaining a threshold stress condition were demonstrated as a suitable agro-management practice to induce flowering in mangosteen. Mangosteen trees subjected to the stress conditions that induced leaf water potential of –0.93 to –1.08 MPa followed by either 1.85 times the total daily evaporation every 3rd day or by an initial application of 35 to 40 mm of water per tree and half of the initial rate applied at 7-day-intervals until flowering produced the largest amount of flowers and fruits.

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ABA	Abscisic acid
BA	6-benzyladenine
df	degrees of freedom
DNA	Deoxyribonucleic acid
DW	Dry weight
e	Exponential index, base of natural logarithm (2.7183)
Eq.	Equation
F	Variance ratio
G	Rate of approach to the maximum rate of photosynthesis
GA	Gibberellin or gibberellin-like substance
GA_3	Gibberellin A_3
GA_{4+7}	Gibberellin A_{4+7}
GDH	Glutamate dehydrogenase
G6PDH	Glucose-6-phosphate dehydrogenase
g_s	stomatal conductance (mmol m^{-2} s^{-1})
IAA	Indole-3-acetic acid
L	Maximum leaf length (cm)
LA	Area of an individual leaf (cm^2)
LAR	Leaf area ratio (total leaf area relative to total plant dry weight, m^2 kg^{-1})
LD	Long day
LDP	Long-day plant
LWR	Leaf weight ratio (leaf dry weight relative to total plant dry weight)
MS	Mean square
NAA	Naphthalene acetic acid
P_n	Photosynthetic rate (μmol CO_2 m^{-2} s^{-1})
$P_{n(max)}$	Maximal photosynthetic rate
PAR	Photosynthetic active radiation
Pfr	Far red-absorbing form of phytochrome
6PGDH	6-phosphogluconate dehydrogenase
PPFD	Photosynthetic photon flux density (μmol photon m^{-2} s^{-1})
Pr	Red-absorbing form of phytochrome
Ptotal	Pr + Pfr

RH	Relative humidity (%)
RNA	Ribonucleic acid
RuBP	Ribulose 1,5-bisphosphate
RWR	Root weight ratio (root dry weight relative to total plant dry weight)
S	Asymptotic maximum photosynthetic rate
SD	Short day
SDP	Short-day plant
SLA	Specific leaf area (individual leaf area/leaf dry weight, $cm^2\ g^{-1}$)
SS	Sum of squares
SWR	Stem weight ratio (stem dry weight relative to total plant dry weight)
TPF	Time to produce the first flowering (years)
W	Maximum leaf width (cm)
WP	Water potential (MPa)

CHAPTER 1

INTRODUCTION

1.1 Definition

Merriam-Webster collegiate dictionary defines juvenile (*adj.*) as physiologically immature or undeveloped, or (*n.*) a young individual resembling an adult of its kind except in size and reproductive activity. To distinguish between the juvenile and mature phase, the term **maturation** has been used to describe the transition from the juvenile to mature phase, and the term **aging** has been introduced to indicate the loss of vigor (Zimmermann, 1972). Fortainer and Jonkers (1976) have used the term **ontogenic aging** to refer to maturation, and **physiological aging** to indicate the loss of vigor. Zimmermann (1973) has suggested that maturation occurs only in the development of seedling plants while plants propagated vegetatively from sexually mature trees undergo aging as well as maturation. In contrast, Leopold (1980) pointed out that processes between juvenility and maturation with the passage of time have been identified as aging whereas, senescence may be defined as the deterioration processes beyond maturation that are natural causes of death. Some of the changes during aging are related to, or are an extension of, the processes involved in maturation (Borchert, 1976). In plants both aging and maturation must take place before the occurrence of flowering.

The juvenile phase in woody plants is described as a physiological period when plants are able to undergo vegetative growth but are unable to perform reproductive activity when exposed to favorable inductive conditions. The mature phase is achieved when plants attain and maintain the ability to produce flowers under favorable

management and environmental conditions (Bernier et al., 1981a; Hackett, 1985). Once a plant attains the reproductively mature condition, flowering will continue as long as a favorable flower-inducing treatment is imposed or exists in nature. However, certain environmental conditions (Heild et al., 1966) or growth substance treatments (Pharis and Morf, 1967) will cause transient precocious flowering in some plants such as seedlings of citrus and conifer, respectively. Grapefruit seedlings produce precocious flowering when appropriate low temperatures are applied, but the plants soon revert to a nonflowering condition and do not produce flowers again for several years (Heild et al., 1966). Plants that produce flowers transiently as a result of a treatment, but cannot maintain the ability to flower under natural or imposed environmental conditions would not be considered reproductively mature. Therefore, attainment and maintenance of the ability or potential to flower when exposed to a normal, natural or imposed, flower-inducing treatments are the only consistent criteria available that indicate termination of the juvenile phase.

Length of juvenility may vary from 20 to 30 days in *Rosa* spp. or up to 30 to 40 years in *Fagus sylvatica* (Clark, 1983). Juvenile plants often have morphological and anatomical as well as physiological and biochemical characteristics, such as characteristic leaf shape and thickness, thorniness, phyllotaxis, pubescence, branch number, branching pattern and canopy structure, shoot growth vigour, ability to form adventitious roots and buds, and partitioning of photoassimilates into main stems or branches, and disease and cold resistance (Bauer and Bauer, 1980; Goodin, 1964; Greenwood, 1984; Greenwood et al., 1989;Hood and Libby, 1980; Libby and Hood, 1976; Sweet and Wells, 1974; Zagory and Libby, 1985; Zimmermann, 1972). Most of these characteristics change gradually during the period preceding the mature phase, and no distinct change in any characteristic

is apparent at the time that the ability to flower is attained. However, stability in these characteristics is often associated with the transition from juvenile to mature phase for individual species.

There are various theories proposed to quantify the termination of juvenile period. In a very approximate way, the length of juvenility is related to the ultimate size of the plant. Zimmermann (1973) demonstrated that transition to the mature phase of *Malus hupehensis* (Pamp.) Redh. was closely correlated with node number. Purvis (1934) postulated that a minimum number of leaves was required before floral initiation could occur. It was demonstrated that the upper and peripheral parts of a plant were the first to obtain mature characteristics, flowering ability, while basal and interior parts retained juvenile characteristics (Longman, 1976). In pecan (*Carya illinoinensis* (Wangh.) Koch.), Romberg (1944) showed that anthocyanin formation was a phase change related character, and interestingly, pigment formation extended about the same distance, from ground level, in the different branches of the same tree. Similarly, the trunk and basal portion of main branches of citrus trees retain thorned ability, whereas the upper and peripheral region are nearly thornless (Soost and Cameron, 1975). The transition from juvenile to mature phase for several plants appear to occur when a photosynthetic leaf area sufficient to sustain flowering and fruiting is attained (Schwabe, 1976; Wareing and Frydman, 1976).

Mangosteen seedlings are slow growing with a long juvenile period. When compared to other tropical fruit trees, such as durian (*Durio zibethinus* Murr.), mango (*Mangifera indica* L.), and rambutan (*Nephelium lappaceum* L.), mangosteen exhibits a

long juvenile period with trees grown from seeds taking from 10 to 15 years to flower (Moncur, 1988; N. Ponchua, personal communication 1992; Richards, 1990). The long juvenile period is a serious constraint to commercialization of this crop due to the high establishment costs.

1.2 Factors controlling the juvenile-to-mature transition

1.2.1 Genetic basis of phase change

The length of the juvenile phase is genetically inherited, although it can be influenced by different factors (Greenwood, 1984; Greenwood et al., 1989; Hansche and Beres, 1980; Snowball et al., 1994a; Teich and Holst, 1969; Visser, 1965, 1976; Way, 1971; Zimmermann, 1976). Shortening the juvenile phase by selecting and breeding has been demonstrated with apple and nut species. Some parents produce offspring with very short juvenile periods of 3 to 4 years from seeds, while others produce offspring with longer juvenile periods of 10 years or more. Inheritance of this character is quantitative. Mehlenbacher and Smith (1992) demonstrated that the use of precocious parents was more effective than sucker removal in shortening the juvenile period of hazelnut. Visser (1964, 1965) showed that the attainment of the flowering condition in apple and pear seedlings was associated with the attainment of a certain size, irrespective of whether this size is attained sooner or later while under the influence of environment. Within a progeny population, the most vigorous seedlings were likely to attain flowering size in the shortest time. Also, investigations by Visser (1970) showed that there was a significant negative correlation between the duration of the juvenile phase and the vigour of the seedling. This criterion can be used to select the short juvenile period seedlings,

although Zimmermann (1977) suggested that plant vigour was not a valid predictor of precocity in pear seedlings.

Hansche (1986) has provided evidence that considerable genetic variation for the juvenile period exists in peach and nectarine breeding stocks. In avocado (*Persea americana* Mill.) time to first flowering and flowering age of various progeny populations was different although there were no differences between self-pollinated plants (Lavi et al., 1992). In an analysis of two complete half-diallele schemes of crosses involving 22 apple and 33 pear progenies, Visser (1976) had a highly significant general combining ability, and nonsignificant specific combining ability variance for the juvenile period. This indicated that inheritance of juvenile period was largely additive in nature. Mode of inheritance is a function of multigenic factors governing development. Recently, Bell and Zimmermann (1990) indicated that length of the juvenile period in pear seedlings was predominantly under additive genetic control, and the selection of parental material with short juvenile periods resulted in a significant reduction in mean juvenile period within the breeding population. Breeding has also led to the production of dwarf plants with shorter juvenile periods and increased productivity (Hansche and Beres, 1980).

1.2.2 Physiological and biochemical basis of phase change

Zimmermann (1973) showed that the node to exhibit first flower was relatively constant under various environments, which influenced growth rate of crabapple (*Malus hupehensis*). Using such an approach, the chronological age in flowering of seedlings of *Lunaria biennis* L., *M. hupehensis*, *Larix leptolepis* Gord., *Ribes nigrum*, and *Betula*

verrucosa was reduced after favorable environment and treatments to induce continuous and/or vigorous growth were applied (Higazy, 1962; Zimmermann, 1971; Robinson and Wareing, 1969; Longman and Wareing, 1959). Longman and Wareing (1959) have been shown that birch seedlings grown continuously under long days in the greenhouse produced flowers when they were 2 m high and less than 1 year-old. On the other hand, seedlings exposed to short day-induced dormancy, followed by chilling-to-break dormancy did not produce any flower after six cycles covering of a period more than 2 years. This indicates that achieving a minimum size may be more important in completing the juvenile period than age or dormancy cycles. An experiment with black currant (*Ribes nigrum*) by Robinson and Wareing (1969) showed that phase change was correlated with, but not dependent on, attainment of a certain size. Visser (1964) also demonstrated the importance of size in attaining the mature condition and concluded that conditions that promoted growth reduced the length of juvenility. However, Visser (1970) and de Veries (1976) indicated that apple, pear, and rose plants possessing a short period of juvenility were smaller at the time of flowering than those with a long juvenile period. Thus, rapid growth may not be the only factor contributing to a short juvenile period.

It is not yet clear what component of size is critical for the attainment of maturity. It could be that with the attainment of critical size, a plant transmits one or more signals to initiate a phase change at the apex. On the other hand, the apical meristem could act independently and undergo the phase transition at a particular time. If the phase transition at the apical meristem is determined by signals when a certain size is achieved, grafting juvenile scions onto mature bearing trees should accelerate or induce their phase

Gibberellin A_3 (GA_3) treatment causes reversion of leaf shape from the mature to the juvenile form in *Hedera canariensis* and *H. helix* L. (Goodin and Stoutemyer, 1961; Robbins, 1957, 1960; Rogler and Hackett, 1975), and coconut (*Cocos nucifera* L.; Schwabe, 1976). Cooper and Peynado (1958), Crane et al.(1961), and Griggs and Iwakiri (1961) have also shown that thorniness in *Citrus* spp., almond, apricot, plum, and pear is increased by GA_3 treatment of mature trees. There is also a change in phyllotaxis in GA_3-treated mature shoots of *H. helix* L. from the mature spiral to juvenile distichous arrangement (Hackett et al., 1987). It seems that high level of GA-like substances might be one character of juvenility. Wareing and Frydman (1976) hypothesized that levels of root-produced GAs in the shoot apices would be expected to decline as tree height and the distance between shoot apices and roots increased, until the ability to maintain the juvenile phase no longer existed and the phase change could occur. Thus, low levels of GA-like substances may be a necessary condition for the transition from the juvenile to the mature phase in some plants. Exogenous application of plant growth retardants to suppress GA biosynthesis can be a strategy to promote maturation. Reports on the effects of plant growth retardants on maturation, however, are conflicting and range from promotive to no effect to inhibitory. These differing results could be related to the content, distribution, and form of GA, which are influenced by environmental factors as well as age of treated seedlings. It was shown that although chlormequat application inhibited growth of English ivy (Frydman and Wareing, 1974) and promoted precocious flowering of birch (Arshad, 1980 cited in Hackett, 1985), levels of GA-like substances increased. These results suggest that plant growth retardants can not always be used to

determine whether declining GA level in the shoot apices are required for the juvenile-to-mature transition.

Arshad (1980 cited in Hackett, 1985) found that girdling of birch caused rapid and large increases in abscisic acid (ABA), but decreases in GA-like substances in the bark and buds above the girdle. This suggests that ABA, an anti-GA, could be involved in phase change in birch and perhaps other species. Walton (1980) suggested that the relationship of size and complexity to phase change in birch might be mediated through a competition for water, and the resultant stress caused increases in ABA level in meristems. Zimmermann (1978 cited in Hackett, 1985) reported that water conductivity of the xylem decreased from the base to the top of the main stem, from main stem to branch, and from branch or twig to the leaf due to constriction of the xylem. The lower the conductivity, the steeper the required pressure gradient to move water through the xylem to target organs. Lowest osmotic pressures are always found in leaves. During drought conditions, pressures in the most peripheral parts of the trees will be the lowest. Gradients in pressure should be greater for large trees than for small trees, therefore stress conditions would be likely more severe in larger than smaller trees. It is generally accepted that the level of endogenous ABA increases significantly in leaf tissues and, to a lesser extent, in other tissues upon exposure to water stress (about 0 to −1.0 MPa) (Bradford and Hsiao, 1982; Salisbury and Marines, 1985; Walton, 1980). However, it is not clear whether the difference in tensions in the periphery of large and small trees is sufficient to implicate differential production of ABA as a mechanism for inducing maturation.

Sink strength of various tissues is constantly changing during growth and development of the plant. During vegetative development, young leaves as well as juvenile plants are very strong sinks. When flowers or fruits are produced, assimilates are translocated to serve the developing flowers or fruits (Turgeon, 1989; Weaver and Johnson, 1985). Therefore, photoassimilate accumulation or diversion to plant organs, i.e., shoot meristems, might be related to size and complexity and to maturation. Environmental treatments that enhance growth rate and early flowering of juvenile plants are the same as those that enhance photosynthesis. It is well established that auxins, cytokinins, and GA promote the mobilization of assimilates by creating metabolic sinks, and may create competition among sinks for assimilates (Goldschmidt et al., 1985; Hackett, 1976; Sachs, 1977; Wareing and Patrick, 1974). Hackett (1976) suggested that hormonal control of assimilate partitioning might be involved in phase changes. Allsopp (1968) and Franck (1976) showed that the change in morphological character during phase change in several plants, e.g. leaf shape, and leaf or branch arrangement, was associated with an increase in the size of the shoot apical meristem. This was supported by the anatomical studies of Stein and Fosket (1969), that showed a large apical area in mature compared to juvenile English ivy. The implication is that during transition to the mature phase, the mature apex has greater competitive ability to attract assimilates than the juvenile apex. Therefore, Allsopp (1954, 1968) hypothesized that nutrient diversion caused alterations in the pattern of apical activity in the juvenile-to-mature transitions.

The experimental evidence discussed above suggests that both hormonal and nutritional factors may be involved in the transition from the juvenile to the mature phase. Although the mechanism(s) to control phase change and why attainment of

minimum size is correlated with transition to the mature phase are not clear, it is clear that the meristem does not act autonomously, and its transition can be influenced by other tissues in the plant.

1.2.3 Morphological and anatomical basis of phase change

Passecker (1949 cited in Leopold and Kriedermann, 1975) showed that the gradient of juvenility decreases from the basal and interior parts to the upper and peripheral parts of a fruit tree. Therefore, the upper parts obtain mature characteristics first, whereas the basal parts retain juvenile characteristics. This observation was confirmed in an experiment with birch (*Betula verrucosa* Ehrh.) seedlings where the upper parts of stem flowered profusely, whereas the branches near the base did not flower when plants were grown under continuous light, high temperature, and high nutrition conditions which induced maximal growth (Longman, 1976). Soost and Cameron (1975) also demonstrated that the trunk and basal portion of main branches of citrus seedlings retained thorniness, while the upper and the peripheral regions were nearly thornless. Similarly, high rooting potential which is a juvenile characteristics can be observed on cotyledonary nodes of *Eucalyptus grandis* rather than on the fifteenth node (Paton et al., 1970). Observations of leaf form in English ivy by Wareing and Frydman (1976) have shown that 3- or 5-lobed, palmate leaves are juvenile characteristics, while entire, ovate leaves are characters of mature ivy.

Zimmermann (1971, 1973) showed that crabapple transition to the mature phase was correlated with node number rather than with plant height. The phase change at the shoot apical meristem occurred in the more distal parts of the plant, than in the basal parts

of the plant. Since leaf initiation (node number) is an activity of the apical meristem, while internode length and height are activities associated with subapical meristems, this finding suggests that cell division activity in the apical meristem rather than in the subapical meristem is related to maturation.

Allsopp (1954) demonstrated that transition to mature morphological characteristics in several plants is correlated with an increase in size of the shoot apical meristem. This relationship is supported by anatomical work in English ivy by Stein and Fosket (1969). It was shown that mature apices had a meristematic area twice as large as the juvenile apices. However, another experiment with ivy plants in which phase change from mature to juvenile was induced by GA_3 application it was shown that there was a change in phyllotaxis to the juvenile configuration before any significant reduction in the area of the apical meristem occurred. This finding appears to exclude the size of apical meristem as a determining factor in phase change, at least during rejuvenation.

1.2.4 Molecular basis of phase change

Some studies in phase change indicate that the apical meristem acts as an autonomous unit and determines mature transition at a particular time, while other studies indicate that the rest of the plant influences the phase change. Both may occur, but the transition itself requires some intrinsic changes in the apex. Milikan and Ghosh (1971) demonstrated less total ribonucleic acid (RNA) content and ribosomal RNA on a dry weight basis in mature than in juvenile leaf tissue of *Hedera helix*. It was also reported that total level of RNA per cell in callus derived from juvenile stems were higher than from mature stems (Hackett et al., 1964). Domoney and Timmis (1980) found no

differences in redundancy ribosomal RNA genes in deoxyribonucleic acid (DNA) of juvenile and mature *H. helix* tissues. Using DNA-RNA hybridization technique, Rogler and Dahmus (1974) also found no qualitative differences between species of RNA in both juvenile and mature apices of ivy. However, differences were observed in the frequency distribution of RNA species, indicating that differences in the rate of transcription of specific genes may be involved in phase change.

To determine the DNA content of mature and juvenile *Hedera helix*, various methods have been used to examine different tissues. Some workers found that some DNA sequences transcribed in the adult phase appeared to be inactive in the juvenile phase. Schaffner and Nagl (1979) examined cells of whole buds and leaves and concluded that nuclei of mature cells contained more DNA than those of comparable juvenile tissues. However, when the leaf tissues were examined Kessler and Reches (1977) and Milikan and Ghosh (1971) found higher DNA content in juvenile phase leaves than in mature phase leaves on a cellular or dry weight basis. There were no differences in DNA content per cell between juvenile and mature tissues taken from shoot apices, apical buds, apical meristem, and stem callus (Domoney and Timmis, 1980; Hackett et al., 1964; Polito and Alliata, 1981; Wareing and Frydman, 1976). Result from a study in quantitative nuclear cytology of ivy also suggested that the amount of DNA per cell is not different for juvenile and mature tissues in *Hedera* (Polito and Chang, 1984).

Fukasawa (1966) used electrophoretic separation techniques to investigate protein from juvenile and mature stem callus of *Hedera* and found several different protein bands. Some of them were denser in mature callus extracts while one was denser in

juvenile extracts. Snowball et al. (1991) using immunological techniques to determine differences in protein quantity during phase change of *Citrus*, demonstrated that there was greater quantity of protein in tissues of mature plants than in the juvenile plants. This was referred to as the 'mature' protein, which was resistant to temperatures up to 80°C and had a molecular weight of approximately 59.7 kDa. The protein increased in the leaves towards the apex of single-stemmed seedlings and in the shoots that were precociously flowering. Its presence preceded the mature phase, indicating that the 'mature' protein may play an important role in the control of phase change in *Citrus*. Greater activity of soluble peroxidase was found in mature avocado leaf tissue compared to juvenile avocado, however the activity of membrane-bound as well as ionically and covalently bound peroxidase showed no marked changes (Sanchez-Romero et al., 1993). They also suggested that since there were large fluctuations in juvenile and mature leaves, use of leaf peroxidase activity as marker of ontogenic age in avocado must be taken with caution. Drouet et al. (1989) showed that glutamate dehydrogenase (GDH) and pentose phosphate pathway enzymes, glucose-6-phosphate dehydrogenase (G6PDH) and 6-phosphogluconate dehydrogenase (6PGDH) appeared to be markers of two physiological systems linked with the juvenile stage of walnut tree growth. Both G6PDH and 6PGDH activities increased while GDH activity was lower in tissues of juvenile walnut. An interpretation is that young organs in juvenile walnut might be characterized by a predominance of the pentose phosphate pathway activity for glucose metabolism.

1.3 Stability of the mature phase

Once the transition to mature phase has been attained, it is relatively stable and return to the juvenile condition does not occur as a result of asexual propagation. There is little understanding about the underlying physiology of the stability, but there are parallels in other systems. The best example is in tobacco pith explants which normally require cytokinin for growth in culture but can be habituated for cytokinin by growing them on cytokinin containing medium or at an elevated temperature (35°C) (Meins and Binns, 1979). When the hormones are removed, the habituated phenotype produces sufficient hormones to sustain its growth, so a new state of cells with different biochemical properties is formed. This new state is stable but becomes nonhabituated (cytokinin requiring) after 7 subcultures. However, the cytokinin-habituated state in tobacco always reverts to nonhabituated state when the plants are regenerated adventitiously. The ability to flower and vegetative characters of explants also indicate that juvenility and maturity are conditions perpetuated within individual cells. Moreover, they persist after removal of cells from the parent plants. Stem callus regenerating from stem tissues of juvenile or mature ivy consistently develop different characteristics. Juvenile callus produces shoots which can be detached and re-rooted to form a new plant while mature callus produce embryos.

If there are intrinsic differences, which form the basis of stable phenotypic characteristics in apical meristems of juvenile and mature plant, these differences would be expected to be reflected in either quantitative or qualitative differences in DNA, RNA, or protein. However, the available results are inconsistent even from within the same plant species, such as *Hedera helix*. Therefore, elucidation of the factor(s) controlling the

juvenile-to-mature transition and the stability of the two phases is difficult. Future research is required to better understand phase changes.

1.4 Procedures to reduce length of juvenile phase

1.4.1 Effects of environmental factors on length of juvenile phase

Several workers have observed that juvenile plants require a certain minimum size or age to attain the mature phase. For practical purposes, the main objective of environmental treatments is to bring juvenile plants to a certain size or height as rapidly as possible. The plant is then enabled to initiate its first flowering or in other cases be exposed to specific flower inducing treatments after achieving a certain size. Treatments successfully used to promote rapid continuous growth depend on plant species and the feasibility of modifying the environment. Treatments include long photoperiod, high light intensity, favorable temperatures, and optimal levels of water and nutrients. Treatments that prevent and/or break dormancy are also used. They include defoliation, low temperature, and growth regulator application.

Longman and Wareing (1959) obtained flowering in birch (*Betula verrucosa*) seedlings grown continuously under long days in a greenhouse when they were taller than 2 m and less than one year old. Similar results were obtained with black currant (*Ribes nigrum* L.) seedlings. First flowering occurred if seedlings were grown under long days in the greenhouse for several months until they were 1 m or taller. Also, long day treatment caused crabapple seedlings to grow continuously to 3 m in height and flower in about 9 months (Zimmermann, 1971). Robinson and Wareing (1969) reported that seedlings of Japanese larch grown under long days in the greenhouse attained a height of

3 m in less than 2 years. The plants flowered in 4 years compared to 5 to 10 years for field-grown plants. Growth of *Chrysanthemum* × *superbum* 'Snow Lady' was promoted when grown under short day conditions and flowered earlier when transferred to inductive long day (Damann and Lyons, 1995). Vegetative growth of carambola (*Averrhoa carambola* L.) was promoted when exposed to 16-hour-photoperiod with 360 $\mu mol\ m^{-2}\ s^{-1}$ (400-700 nm) light intensity (Salakpetch et al., 1990), but its effects on precocity has not been determined.

Eschscholzia californica Cham. (Lyons and Booze-Daniels, 1986), *Coreopsis lanceolata* L. 'Early sunrise' (Damann and Lyons, 1993), *Rudbeckia hirta* L. 'Marmalade', and *Gaillardia pulchella* Foug. (Bourke, 1990) exhibited first flowering earliest after transfer to inductive long days if they were previously grown under short days to the 10, 16, 19, and 20 unfolded true leaf stage, respectively. These results led to the suggestion that a specific node count might affect flowering by long day conditions.

Higazy (1962) demonstrated that high light intensity increased early growth of several herbaceous species and reduced the juvenile period, so that seedlings were able to respond to flower inducing treatments at a younger age than normal. Increasing light intensity did not enhance growth of unbranched mangosteen (*Garcinia mangostana* L.) seedlings whereas, branched seedlings exhibited increased growth with increasing irradiance due to an increase in biomass production (root, shoot, and total plant dry weight) (Wiebel et al., 1994).

Reducing time to flowering can be obtained by optimizing growth in the greenhouse, nursery, and orchard. Size of apple seedlings transplanted into the field

conditions is very important for early flowering when field-grown conditions are optimal in terms of soil moisture and nutrient nutrition. By improving growing conditions, time to flowering of genetically comparable groups of progeny was reduced from 7.4 to 4.3 years, and from 9.2 to 6.0 years in apple and pear seedlings, respectively (Visser et al. 1976). Similarly, when continuous growth in the nursery was promoted, time to flowering of grafted durian (*Durio zibethinus* Murr.) seedlings was reduced from 6 to 3 years after transplanting to favorable field-grown conditions (P. Chingsuwanarot, personal communication, 1992). This emphasizes the importance of optimizing growth of seedlings of some woody species at all stages to shorten the juvenile phase.

Zimmermann (1972) demonstrated that low day/night temperatures (20-26°/7°C) induced precocious flowering in grapefruit seedlings (*Citrus paradisi* Macf.). Flowering in 2-year-old pine seedlings was stimulated after transferring from freezing to warm temperatures, followed by heavy fertilization. Aldwinckle (1975) showed that flowering of 26-month-old apple seedlings was promoted by defoliation (a method to break dormancy) compared to 4 years after germination that for seedlings grown under normal field conditions.

1.4.2 Influences of treatments that retard growth on length of juvenility

Girdling or ringing the stem by removing a band of bark, scoring with a knife or twisting a fine wire around the stem, bark inversion, grafting on dwarf interstocks, root pruning, water stress, and growth retardant application are treatments that retard growth and can promote flowering in reproductively mature trees of some species. Several investigations with conifers have shown that stress treatments e.g., water stress, high

temperature, as well as low soil oxygen levels, induce precocious flowering in juvenile plants. However, there is no evidence that such treatments reduce the length of the juvenile phase. Several experiments indicate that girdling and scoring are effective for promoting early flowering in apple, pear, and sweet cherry seedlings. Way (1971) demonstrated that scoring was more effective in inducing flowering on older than younger apple seedlings. Zimmermann (1972) suggested that such treatments are effective, because juvenile plants are probably in the transition phase.

Other workers have reported negative results. Fritzsche (1948 cited in Zimmermann, 1972) was able to obtain early flowering only on branches in the adult stage or in the transition from juvenile to mature stage after girdling 4 to 11 year-old apple seedlings. Stephens (1964) reported that both scoring and girdling did not promote flowering in 14-year-old white pine seedlings however girdling had a promotive effect on branches of 22-year-old seedlings.

Sax (1957) showed that bark inversion was able to induce early fruiting on young grafted apple trees. He also found that tying knots on the stems of both seedlings and grafted apple trees caused growth reduction in both cases but promoted fruiting in the grafted trees only. Other workers obtained similar effects on older ungrafted nut trees (Granes, 1956, 1957, 1958 cited in Zimmermann 1972).

1.4.3 Effects of growth regulators and fertilization on reducing juvenile phase

Juvenile cuttings taken from oak seedlings root quite easily, but lose juvenility very rapidly which results in a reduction in rooting capability (Morgan and McWilliams, 1976). GA_3 has been shown to improve rooting capability when applied as a bark

treatment on leafless pruned stems of 3-year-old *Quercus ithaburensis* Deche. (Eshed et al., 1996).

A systematic study of endogenous GA in flowering of *Citrus* spp. revealed that GA_1, a GA_4-like substance, GA_8, GA_{17}, GA_{19}, GA_{20}, GA_{29}, GA_{44}, and Iso-GA_3 were found in elongating shoots and were present at higher concentrations in vegetative than in floral shoots. Moreover, these substances were found at low concentration at the time of floral induction (Plummer, 1987 cited in Mullins et al., 1989; Poling and Maier, 1988). It is well established that GA application inhibits flowering of woody plants. GA_3 and GA_{4+7} have shown to suppress flowering in apple and pear (Buban and Faust, 1982; Looney, 1983; Zeevaart, 1978, 1983), *Citrus* spp. (Goldschmidt and Monselise, 1972), mango (Tomer, 1984), peach (Dennis, 1976; Gianfagna et al., 1986), sweet cherry (Oliveira and Browning, 1993a, b), and black currant (Schwabe and Al-Doori, 1973). To stimulate the juvenile-mature transformation of fruit trees, GAs have been used to stimulate rapid vegetative growth. There were a few instances where GA was able to induce flowering in juvenile plants of certain coniferous species. However, after cessation of application the treated plants reverted back to the juvenile phase.

If endogenous GA is responsible for inhibition of flowering, plant growth retardants, which inhibit GA biosynthesis, might be expected to promote flowering. Exogenous application of chlormequat, daminozide, and benzothiazole-2-oxyacetate has been shown to enhance synchronous flowering in lemon (*Citrus limon* Burm.; Monselise and Halevy, 1964; Monselise et al., 1966; Nir et al., 1972; Salomon, 1981), and sweet orange (*C. sinensis* Osb.; Monselise and Goren, 1969; Lenz and Karnatz, 1975).

Wang et al. (1985) investigated physiological and biochemical changes in apple seedlings cv. York Imperial following paclobutrazol application and concluded that paclobutrazol regulated the partition and utilization of carbon assimilates. It shifted assimilate partition from leaves to roots, increased chlorophyll, soluble protein content and concentration of mineral elements in leaves, and carbohydrate levels in all plant parts. In addition, it enhanced mineral nutrient use efficiency and increased the activity of root respiration. By altering metabolism or metabolic products, paclobutrazol might be able to increase root growth, enhance flowering and fruit set, and improve fruit quality. Paclobutrazol has been shown to stimulate flowering in lychee (*Litchi chinensis* Sonn.; Chaitrakulsap et al., 1992), durian (Chandraparnik et al., 1992), 'West Indian' lime (Snowball et al., 1994b), and mango (Voon et al., 1991). Nagao et al. (1999) also showed that soil-drench application of uniconazole significantly increased flowering in containerized 'Kau' macadamia trees. It seems that once rapid growth in juvenile plants are promoted by either environmental treatments or GA application, growth retardant application can be used to induce precocious flowering.

Sprays of 1000 ppm ethephon (2-chloroethyl) phosphonic acid, an ethylene releasing compound, induced heavy flowering in girdled and ungirdled juvenile mango (Chacko et al., 1974a, b). They concluded that ethephon could be profitably used for early evaluation of hybrid seedlings in a mango breeding program. Volz and Knight (1986) also demonstrated that application of 250 ppm ethephon increased precocity, by inducing more spur buds, in both juvenile 'Bramley' and 'Cox' apple.

Zimmermann's (1972) review has shown that fertilization is important, by mainly contributing to more rapid growth of juvenile plants and consequently to earlier flowering. Mergen (1961, 1963) succeeded in inducing 2-year-old pine seedlings to flower by transferring the seedlings from freezing to warm temperatures in combination with heavy fertilization. Visser (1970) showed that the size of transplanted seedlings as well as orchard soil moisture and fertility were important for early flowering in apple.

1.4.4 Grafting and girdling induced precocity

Zimmermann (1972) noted that the effectiveness of grafting seedling scions onto dwarfing rootstocks in order to shorten the juvenile phase has been in question for many years because of conflicting reports in the literature. However, Tydeman (1937 cited in Zimmermann, 1972; Tydeman, 1961) demonstrated that seedling scions grafted onto certain clonal apple dwarfing rootstocks flower 2 to 4 years earlier than those on their own roots. In some cases, the scions also showed some mature characteristics e.g., leaf form, and node of branching earlier than on parent seedlings.

Visser (1973) suggested that earlier flowering in apple could be induced by grafting the seedling scions onto similar rootstocks, but this result was attributed to different growth conditions. The better the growing conditions, the smaller the difference between flowering time of seedlings grafted on dwarfing rootstocks compared to those on their own roots.

Early flowering can also be observed when grafting seedling scions onto reproductively mature plants. Zimmermann (1972) has suggested that grafting induces flowering only when scions are in the transitional phase or come from mature seedlings.

However, Singh (1959) obtained early flowering when 1-year-old mango scions were grafted onto mature plants. A similar result has also been obtained in durian (P. Vejachewa, personal communication). This technique has been widely used for breeding purposes in Thailand.

The mature state is relatively stable during vegetative propagation. Some propagation techniques, however, can cause an increase in vegetative vigor and delay flowering. These responses are usually interpreted as changes in physiological rather than ontogenic age. Citrus experiments by Monselise (1973) showed that grafting mature calamondin (*Fortunella* sp., *Citrus reticulata*) scions onto juvenile sour orange (*C. aurantium* L.) rootstocks led to greater vegetative vigor and a delay in flowering. Revision to the juvenile condition by grafting on juvenile rootstocks has also been documented in *Hedera helix* L., *H. canariensis, Eucalyptus platyphylla, E. camaldulensis, Terminalia superba,* and *Cupressus dupreziana* (Hackett, 1985). In contrast, Navarro et al. (1975) demonstrated that *in vitro* micrografting of mature shoot apices onto virus-free apomictic seedlings had no effect on the maturation of the resulting plants. Other studies have shown that grafting mature scions onto juvenile rootstocks can reduce time to flowering in durian, mango, santol (*Sandoricum indicum* Cav.), longkong (*Aglaia* spp.), and jackfruit (*Artocarpus heterophyllus* Lamk.) when compared to ungrafted seedlings (P. Piyarom, personal communication, 1995).

Although girdling does not induce precocious flowering in seedlings of all fruit crops, it is effective for some species. Fruiting of apple seedlings can be hastened by girdling with a herbicide as well as by mechanical ringing or scoring (Way, 1971).

Lahav et al. (1986) reported that girdling was a method for shortening the juvenile period of 3-year-old avocado seedlings. Girdling (Fogle, 1975; Sherman and Lyrene, 1983) also induced precocious flowering in 3 to 4-year-old sweet cherry and citrus seedlings. Since it is possible to produce pistillate flowers on shoots of juvenile pecan clones by girdling, Thompson (1986) suggested that this technique can be used to induce precocity of pecan in a functional breeding program with a 2 year generation time.

1.5 Flowering process

Flowering involves a dramatic sequence of changes at the shoot apex or the axillary meristems. It is an integrated process, involving ecophysiology to biophysics. Bernier (1988) describes the flowering process as divided into two major phases, initiation and development. These two phases respond to different environmental and internal variables.

1.5.1 Floral evocation and morphogenesis

1.5.1.1. Floral evocation

Events occurring in the apex of the plant from exposure to favorable inductive conditions until appearance of the first signs of flower initiation are termed ***floral evocation*** (Bernier, 1986; Evans, 1969). Since several experiments to induce precocity in juvenile plants by grafting the juvenile scions onto mature trees have not been successful (Robinson and Wareing, 1969; Wareing, 1987), this suggests that the phase change (competence) from juvenile to mature in such plants is determined by some intrinsic mechanism in the apex (Wareing, 1987). However, it is difficult to identify the characteristics that are associated with or are critical for the attaining of competence or

the capability of responding to floral inductive conditions. Cells may be competent for a specific inductive signal for only a limited time period. Once the meristematic cells become competent and react to an inductive signal(s) the cells are destined for a new or more restricted developmental fate (McDaniel, 1984, 1989). Although the molecular basis for competence is unknown, some changes following induction period can be detected. For example, the cells may change their morphology and plastochron index, establish a phyllotactic pattern, synthesize a new protein, activate specific enzymes, and change the capacity to respond to growth substances (Bernier, 1988; Bernier et al., 1981b; McDaniel, 1984, 1989).

Bernier et al. (1981b) have proposed that there are many events occurring after the exposure of the plants to favorable inductive conditions. These sequence of events, are essential for flower initiation. Furthermore, it is not a single sequence of events but multisequentially events. Although the different sequences may be independent initially, they interact at a later step during floral initiation. This has led to the suggestion that interaction is essential for the evocational process to proceed to a point where the meristem is irreversibly committed to initiate flowers. The sequences of evocational events can occur at all levels of organization, from the molecular to the morphological level. They each start at a particular time after the beginning of induction. Molecular or subcellular events occur first, followed by cellular and morphological events. Increase in RNA and protein synthesis, in respiratory substrates and respiration rates, and in activity of several enzymes e.g., invertase, phosphatase, and succinic dehydrogenase as well as mitochondria number are evocational events that occur at the molecular or subcellular level. Cell synchronization, increase in the rate of cell division and cytoplasmic matrix,

as well as a decrease in cell doubling-time are cellular events occurring during the evocational process. The changes in shape of meristem to a dome shape and the precocious initiation of axillary meristems are examples of morphological events occurring before initiation of the first flower (Bernier, 1986, 1988; Bernier et al., 1981b). Bernier et al. (1981b) suggested that the complete sequences of evocational events may occur in some species under favorable inductive conditions, while incomplete sequences of events may take place in unfavorable conditions. They also indicated that not all shoot apices can react to conditions that promote flowering.

Floral evocation may start at different times in different species. For a plant that requires only one photoinductive cycle, the onset of movement of the leaf-generated floral stimulus can be assumed as the start of evocation. But some plants e.g., spinach, *Xanthium*, and *Sinapis* have an intermediate meristem and dramatic changes in the meristem occur long before the onset of stimulus movement (Bernier et al., 1981b; Vince-Prue and Gressel, 1985). The end of evocation is much easier to determine. The point at which commitment of the meristem to flower becomes irreversible is considered as the end of evocation or the period of floral determination. This point occurs at about the time most histological and morphological changes start and before the first sign of floral initiation (Bernier et al., 1981b; Bernier, 1986). Evocation is essentially a molecular and cellular process whose completion triggers the changes at higher levels of organization.

1.5.1.2. Floral morphogenesis

After the completion of multisequential events in the evocation process, the growth pattern of apical meristem is profoundly changed. Bernier (1988) suggested that

some changes in the apical meristem are common to many plants, and others are specifically related to the reproductive structures that are be formed. The components of processes that determine floral morphogenesis include meristem shape and size, rate of appendage production, leaf growth, precocious initiation of axillary meristems, internode growth, and decrease in primodium size and phyllotactic changes.

The earliest and most common change in meristem shape is doming which is partly attributable to the vacuolation and elongation of cells in the pith-rib meristem (Bernier, 1988; Bernier et al., 1981b). Later, shape and size changes in the meristem are clearly related to specific features of reproductive structures (Bernier et al., 1981b; Cottrell et al., 1981; Kirby, 1974; Marc and Palmer, 1982; Moncur 1981; Pharis et al., 1987). Cottrell et al. (1981) and Pharis et al. (1987) suggested that GA is most likely a factor involved in the elongation of the grass apex. Maksymowych et al. (1976) also showed that GA_3 application increased the meristem size in *Xanthium*. A nutritional factor is also necessary in the enlargement of many transitional meristems (Bernier et al., 1981b; Lyndon, 1977). The meristems of some species however, may become smaller at the transition and others may stay the same size.

An increase in the rate of appendage initiation is often detectable (Bernier et al., 1981b; Lyndon and Battey, 1985). Each time a meristem initiates on appendage, the growth of internodes is increased. Internode growth is a common event in transitional apices of both caulescent and rosette plants (Bernier et al., 1981b). However, after cessation of leaf initiation and when reproductive structures are formed, a dramatic shortening of the plastochron index occurs (Bernier et al., 1981b; Lyndon and Battey,

1985). Shortening of the plastochron can be obtained by application of various plant growth regulators, e.g. GA in *Xanthium, Arabidopsis, Perilla,* and *Rudbeckia* (Bernier et al., 1981b; Besnard – Wibaut, 1981; Maksymowych et al., 1976), cytokinin in *Chenopodium, Arabidopsis,* and *Sinapis* (Bernier, 1988; Besnard – Wibaut, 1981; Seidlova and Krekule, 1977). In addition, the last leaf before the formation of reproductive structures are generally small with a simple shape due to a strong inhibition of primordium growth, and several factors were found to affect this change (Bernier et al., 1981b), among which GAs and cytokinins are prominent (Engelke et al., 1973; Halperin, 1978; Maksymowych et al., 1976; Pao and Morgan, 1986).

Initiation of axillary meristems to form either flowers, spikelets, or inflorescence branches is critically important for floral transition. Release of axillary meristems is presumably related to a loss of apical dominance, and changes in hormonal and nutrient factors, which are involved in apical dominance. Antagonistic results of auxins and cytokinins in controlling apical dominance have been reported in *Chenopodium* and grapevines (Mullins, 1980; Seidlova and Krekule, 1977). Seidlova and Krekule (1977) suggested that the inhibitory effect of exogenous IAA on flowering of *Chenopodium* could be explained on the basis of its effect on strengthening apical dominance. In grapevine, cytokinins have been shown to be essential for formation of branching and inflorescences (Mullins, 1980).

Although there is an increase in the relative size of the meristem to that of its appendages during the transition to flowering, a reduction in primordium size occurs when a flower is formed (Lyndon, 1977; Lyndon and Battey, 1985). This decrease in

primordium size is a critical change and basic to the increased complexity in phyllotaxis (Lyndon, 1977). Maksymowych et al. (1976) demonstrated that GA_3 application can decrease primordium size and alter the phyllotactic pattern of *Xanthium* leaves in a manner very similar to that appearing during the transition to flowering.

Number and fusion of floral organs are considered as fixed characters in the flowers of many species. Organ fusion has been suggested as a unique aspect of floral morphogenesis. The number for each type of floral organ is fixed in the flowers of many species, especially in flowers with a small number of appendages (Bernier, 1988; Kinet et al., 1985). Flowers of some species have large and indefinite numbers of at least one class of each appendages. Also, modification or aberrant appendage number, due to meristem misfunctioning and transformations of appendages from one type to another, is common in flowers. From these observations, Kinet et al. (1985) concluded that the pattern of floral morphogenesis is never absolutely fixed and the control of the processes is not perfect. It is clear that the fate of a primordium cannot be entirely predicted from its site of initiation because extra appendages may arise in unusual places in aberrant flowers. Control mechanisms over fusion of floral organs is still unknown but Verbeke and Walker (1986) suggest that *Catharanthus* requires both physical contact and a diffusible unknown compound for fusion of initially free carpel primordia.

Based upon the components and processes of floral morphogenesis, floral and vegetative morphogenesis are unique and contradictory. In most cases, the regular production of flowers is the practical way to identify the end point of juvenile phase. The

components of floral morphogenetic processes are useful in determining not only the transition to flowering, but also the transition to maturation.

1.6 Mangosteen

Mangosteen (*Garcinia mangostana* L.), a native to the Malay Archipelago, is a highly regarded fruit in tropical Asian countries. It is referred to as the '*Queen of Tropical Fruit*' and is an esteemed fruit in the Guttiferae family due to its exquisite flavor and eye appeal. The tree is pyramidal shaped and evergreen, attains a height of up to 10 m and possesses opposite, unifoliate, short-stalked and thick leaves. Observations in Thailand indicate that it is a monoecious tree, producing fruit with apomictic seeds (Moncur, 1988; Morton, 1987). Flower buds are formed on the terminals of new growth of small twigs that develop from the main stem or large branches. The fruit, capped by the 4 lobed prominent green calyx at the stem end, has a thick reddish purple pericarp and is divided into 4 to 8 segments. One or two of the segments contain larger seeds. The flesh is snow-white, juicy and soft with a sweet and sour taste (Alexander, 1984).

Mangosteen requires tropical conditions with optimum growing temperatures ranging from 25° to 33°C and RH over 80%. It is adapted to regions experiencing heavy and well distributed rainfall (IBPGR, 1986). Almeyda and Martin (1976) reported that a high water table seems to favor growth.

Statistical data showed that during 1975-1978, only 77,700 tons of mangosteen was produced in Southeast Asian countries, and among those, Thailand was the leading producer (IBPGR, 1986). The majority of the production comes from backyard trees or

trees grown as a minor component in mixed orchards with durian and rambutan. Main production is for domestic consumption only, but a very small amount is exported to neighbor countries.

The world market for horticultural products has expanded significantly over the last five years. Mangosteen has been proposed as a major potential fruit crop due to its exquisite flavor and long shelf life (Anon., 1990). Lucrative markets all over the world can be supplied with this delicacy, but commercial quantities are unavailable to exploit these markets. Taiwan and Japan are large markets for fresh and frozen mangosteen, respectively. Approximately, 67% of Taiwanese imported mangosteen comes from Indonesia, 32% from Thailand, and 1% from others (Tongdee et al., 1997). At present, several thousand mangosteen orchards are being established in Thailand, and several thousand trees are being propagated in tropical northern Australia. The development of an industry, however, is long term since growers will be slow in realizing a return on their investment due to the slow growth of seedlings and the long juvenile phase. Although more than 90,000 tons of mangosteen have been produced in Thailand since 1991, less than 10% of total production is exported fresh or frozen. This is due to both inconsistent quality and production. Translucent flesh and exterior and/or interior latex exudation are generally accepted as serious problems of mangosteen quality. Appropriate agromanagement techniques are required to produce a large marketable yield for mangosteen producing countries.

Vegetative propagation in mangosteen is very difficult. Although successful cleft grating has been reported in Thailand, Australia and Malaysia, the technique has not been developed commercially (Chong and Chai, 1986). Goh et al. (1988, 1990) recently

obtained *in vitro* production of plantlets from immature leaves taken from juvenile and mature trees. Their field performance is being evaluated. Due to the absence of a reliable vegetative propagation method, apomictic seedlings are widely used as planting materials for raising commercial plantations. It is generally accepted that larger seeds produce stronger seedlings with a more well developed rooting system.

Mangosteen is slow growing, and possesses a long juvenile period, probably lasting 10 to 15 years (Kennard and Winter, 1960; N. Ponchua, personal communication, 1992). Downton et al. (1990) observed that frequency of vegetative flushing depended on the age of the plants. Under controlled conditions, flushing intervals of 18-month-old seedlings were 40 to 45 days. Dormant terminal buds are hidden within a cavity at the base of the petioles of the last pair of leaves. Any treatment, which breaks dormancy, can increase the rate of vegetative growth. Wiebel et al. (1992) reported that bud dormancy was broken by GA_3 applied directly to the bud, and the internode length of newly emerging flushes was dosage dependent. Poonnachit et al. (1996) also succeeded in stimulating vegetative flushing by thiourea treatments.

Presently, there is considerable interest in mangosteen as a new potential fruit crop in Asian-Pacific regions due to its reputed taste appeal, long storage life, and durability in transport. However, commercial exploitation has been limited because of its slow growth of seedlings and long juvenile period.

1.7 Problem statements and justification

Mangosteen (*Garcinia mangostana* L.) is considered as one of the most exquisite and valuable fruits of the tropical regions (Hume, 1947). Mangosteen has remained an underexploited tropical fruit and unavailable to major consumer markets outside Asia although it has good transport characteristics, a long shelf life, and consumer acceptance (Almeyda and Martin, 1976). A constraint to the expansion of mangosteen production is the lack of appropriate agrotechniques to improve production in the producing countries. Also, mangosteen has a long juvenile period that impedes commercial establishment. It is also impossible to employ conventional methods of crop improvement by breeding and selection due to the lack of genetic variation and viable pollen in mangosteen (Lim, 1984; Richards, 1990). Molecular biological studies have also been undertaken, however, these studies have not been successful.

Attempts to induce precocity and achieve more rapid growth by grafting onto related species of mangosteen have not succeeded (Hume 1947; P. Polprasid personal communication). Cleft self-grafting is successful and can result in precocious bearing, but the scion always grows slowly and more horizontally (P. Polprasid and S. Chandraparnik, personal communication). These results have discouraged commercial planting of such grafted material.

The length of the juvenile period can be influenced by environmental and genetic factors. Once the ability to flower has been achieved and is maintained, the trees are considered to have attained the maturity. The characteristic features of the transition may involve morphological and anatomical development as well as physiological and biochemical changes. Enhancing the growth rate of apomictic seedlings to achieve a

certain minimum size by providing optimal growing conditions may offer a promising approach to shortening the juvenile period of mangosteen.

The present study will be directed towards characterizing and overcoming juvenility of mangosteen. The overall objectives of this study are to:

1.7.1 Characterize growth in juvenile, transitional, and mature mangosteen trees.

1.7.2 Determine the influence of age and canopy size on the transition from the juvenile-to-mature phase.

1.7.3 Determine photosynthetic characteristics of mature mangosteen trees.

1.7.4 Investigate methods to accelerate growth of juvenile plants.

1.7.5 Investigate agro-management practice to stimulate flowering in mature trees.

CHAPTER 2

CHARACTERIZING GROWTH RATE OF MANGOSTEEN TREES DURING TRANSITION FROM THE JUVENILE-TO-MATURE PHASE

2.1 Introduction

The transition from the juvenile to mature phase of woody plants is associated with increasing size of the tree, changes in the nutritional and other physiological conditions within the tree, increasing age and overcoming bud dormancy. These correlative events may reflect causal relationships, therefore phase change can be promoted by one or more of these changes (Robinson and Wareing, 1969). There is a significant negative correlation between length of juvenile period and the vigor of apple seedling as measured by stem diameter. Stem diameter is one of characteristic feature of phase change in apple and can be used as an effective parameter for selection during the nursery stage. In addition, selection for stem vigor can enhance breeding efficiency by improving the chances of finding precocious varieties (Visser, 1964, 1970).

Classical techniques to describe growth curves of an organism's life cycle are based on the calculation of absolute or relative growth rate from raw data over various periods of time. The functional approach is another possibility. To describe growth patterns by means of a functional approach, mathematical functions are combined in various ways to remove biases when empirically fitting data into different growth phases which occur in the life cycle of any particular organism (Fisher and Heins, 1996). Brody (1945) described the first phase of growth with an exponential function and described the second using a form of Richards' functions. The growth function showed a sudden jump

in the predicted growth rate at the transition between growth phases. Cubic splines were used by Hunt and Evans (1980) to fit growth data of maize (*Zea may* L.) after dividing growth into different phases. The cubic spine fitting ensured smooth transitions between growth phases. In another functional approach to modeling growth, two or more growth phases of some organism or population are summed. Berghage and Hein (1991) summed growth phases of internode length to attain a stem elongation model for poinsettia. Genard and Bruchou (1993) also combined a functional description of growth curves, multivariate exploratory data analysis, and graphical displays to describe the growth of peach fruit. When a function is fitted to growth data, the growth curves can be compared more easily than in the classical approach.

The present study attempts to determine whether increasing size of mangosteen trees in terms of growth rate characterizes the phase change in mangosteen. The growth function to describe the growth pattern of mangosteen was also developed.

2.2 Materials and Methods

Plant material. Mangosteen trees used in this study were between 1 to 24 years-old from seeding, and consisted of ten trees at each individual age. The 1- to 3-year-old seedlings were grown in 5.6 liter black polyethylene bags (152 mm diameter x 305 mm depth), containing 50, 25, and 25% by volume of rice hulls, soil, and chicken or cow manure, respectively, and maintained in a shade house at Chanthaburi Horticultural Research Center. The shade house was covered with 50% black shadecloth which admitted a maximum photosynthetic photon flux density (PPFD) of 598.3 μmol m^{-2} s^{-1}. Annual mean maximum/minimum day/night temperatures were 31.9/23.1°C. The seedlings

were irrigated with an overhead sprinkler system and fertilized every month with 5 g 16N-$16P_2O_5$-$16K_2O$ per bag. The seedlings were rebagged every year.

The trees which were older than three years old were grown under field conditions, such that the trees at age of 4- to 6-years-old and of 16-, 18-, 20-, and 24-years-old were grown in full sun in research plots at 3 locations of Chanthaburi Horticultural Research Center. Trees were planted at 8 x 8 m spacing (156 trees/ha). Trees at age of 7- to 10-years-old were grown in 2 private orchards interplanted with mature trees of rambutan, durian, and *Lansium* spp. in Trad and Chanthaburi provinces along the east coast of Thailand. Trees were planted at 10 x 10 m spacing (100 trees/ha). The soil is mainly sandy loam with pH between 4.5 and 5.5. Annual rainfall is between 2500 and 3500 mm and distribution of rainfall is about 6 months. The elevation is 20 to 30 m above the sea level. The trees at age of 4- to 10-years-old in both research plots and private orchards were irrigated by a sprinkler system and applied by 16N-$16P_2O_5$-$16K_2O$ and cow manure 3 times a year. The application rate of fertilizers was about 500-800 g per tree at each application. A single application of cow manure was applied with the first application of soil fertilizer. The trees at age of 16- to 24-years-old were irrigated by a sprinkler system and fertilized with 2.5 kg per tree each of complete fertilizers, 16N-$16P_2O_5$-$16K_2O$ and 8N-$24P_2O_5$-$24K_2O$, immediately after harvest and 2-3 months later, respectively. During the stage of fruit development (about 1 month after anthesis) , 13N-$13P_2O_5$-$21K_2O$ was also applied to promote growth of developing fruit.

Measurements. A total of 140 trees, 10 trees at each age, were chosen. Tree height measurements for variously aged trees were made from the top to the base of the

canopy. The height was measured at the end of vegetative flush when the last pair of leaves on the latest flush was fully mature.

Statistical analysis. Mathematical functions were used to describe the empirical relationships for each phase. An exponential function was used to describe an increasing growth rate during the lag phase. Constant growth rate during the linear phase was described with a linear function. A monomolecular (negative exponential) function was used to describe the crop growth when the crop reached the asymptote during the plateau phase. The three mathematical functions were then combined as a logistic continuous function, to describe the different growth phases. The logistic function was fitted to 1 to 24-year-old trees, and the resulting height estimates were examined for trends and compared with the actual data. When the actual height was compared to the predicted height, the actual height was obtained from variously aged mangosteen (20 trees at each individual age) grown along the east coast of Thailand other than those used in developing the growth function.

The actual height was also divided into 3 groups; young, near-mature, and mature, representing a particular stage of growth and development of mangosteen. Linear relationships between height and age of those 3 groups were developed to describe the growth rate of 3 different growth phases of mangosteen. The slope (growth rate) of the 3 different growth phases was then compared to determine whether the juvenile-to-mature transition could be distinguished from growth rate. Data were transformed to stabilize the variances of 3 different growth phases before the relative growth rate was compared. Logarithmic transformation, *log(height + 1)*, was used because the standard deviations of

mangosteen height in the present study were proportional to the mean height (Little and Hills, 1978; Snedecor and Cochran, 1980). Comparison of the slopes could be made using the analysis of covarience to compare the differences between the adjusted class means (Snedecor and Cochran, 1980).

2.3 Results

Growth of mangosteen trees, represented by cumulative height in meters followed a sigmoidal pattern over time (Fig.2.1). Height of 1- to 3-year-old young mangosteen trees grown in a 50% black shade house, gradually increased from 0.19 to 0.69 meters. Trees were transplanted to the field in the 3rd year and these plants increased in height to 1.25 meters, when they were 5 years old or about two years after transplanting. Beyond 5 years, height of mangosteen trees increased linearly to 8.88 meters when they were 24-years-old. According to the growth pattern (Fig. 2.1), growth in height of 1 to 5-year-old mangosteen plants could be categorized as a undergoing lag phase. The following exponential relationship could be used to describe this phase.

$$\text{Height} = 0.117e^{0.508age} \quad \text{.....(2.1)}$$
$$r = 0.974^{**},\ n = 5$$
$$r^2 = 0.949$$

A linear phase started from height at 6 to 18 years and a linear relationship could be described with the following equation.

$$\text{Height} = 0.46(age) - 0.407 \quad \text{.....(2.2)}$$
$$r = 0.995^{**},\ n = 7$$
$$r^2 = 0.990$$

A plateau phase began when the trees were 19 years old. When the components of three phases were combined, a sigmoidal growth pattern of mangosteen was derived as follows:

$$\text{Height} = 8.88/(1+52.30e^{-0.407age}) \quad \text{.....(2.3)}$$
$$r = 0.951^{**}\ n = 13$$
$$r^2 = 0.904$$

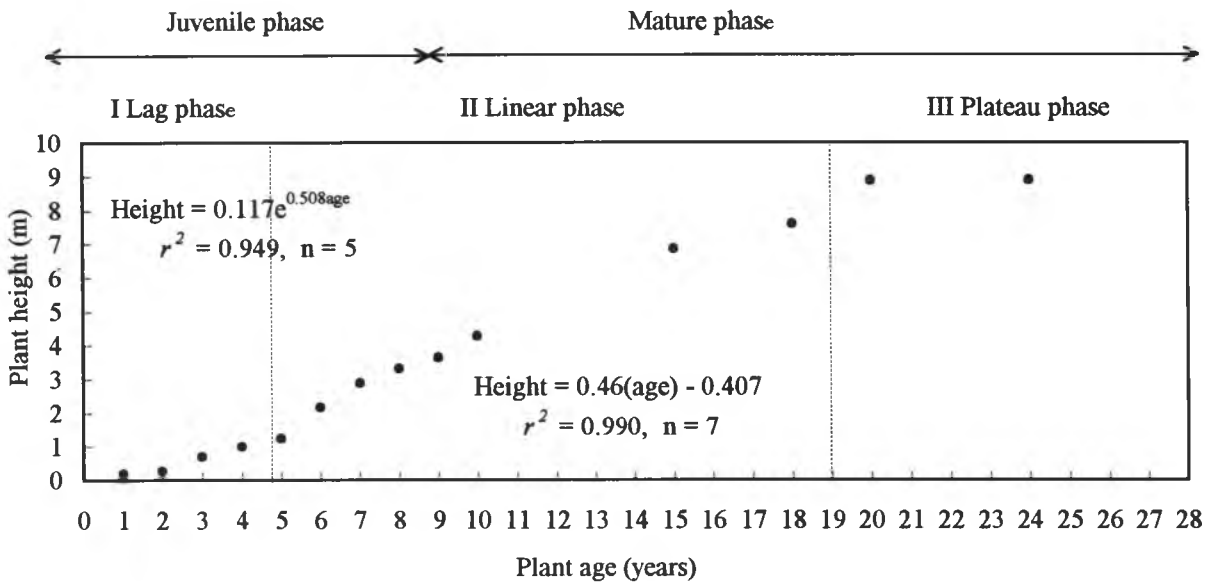

Fig. 2.1 Means of actual heights of mangosteen trees, Chanthaburi, Thailand. Growth pattern of mangosteen trees, represented by height, can be expressed as: Height = $8.88/(1+52.30e^{-0.407age})$, r = 0.951**, n = 13 and r^2 = 0.904

Regression can be applied to predict values on the y-axis from knowledge of the corresponding values on the x-axis. To test how well a nonlinear relationship between height and age of mangosteen, Eq. 2.3, estimated growth of mangosteen trees grown in Thailand, the actual height and the estimated (predicted) height from the above equation were compared. The age in Eq. 2.3 was substituted with the actual age of mangosteen and, the predicted height was then obtained. The relationship between the actual height from the corresponding ages to the predicted height is shown in Fig. 2.2 with an r^2 = 0.97, implying that there was some deviation of the predicted height from the actual height when Eq. 2.3 was used. Subsequently, when the relationship of actual (▲) and predicted (●) height was compared (Fig. 2.3), the predicted height at age for 6- to 8- year- old

trees was underestimated whereas the predicted height from 9- to 11- and from 15- to 20-year-old was overestimated. Both the predicted and actual heights were equivalent at age 24-years. The closeness of relationship in Fig. 2.2 gave a highly significant r^2 and correlation coefficient, $r = 0.98$. The growth equation (Eq. 2.3) can be tested by obtaining height and age data for mangosteen grown in the east coast of Thailand and determining how well the equation predicts height of mangosteen trees of ranging ages.

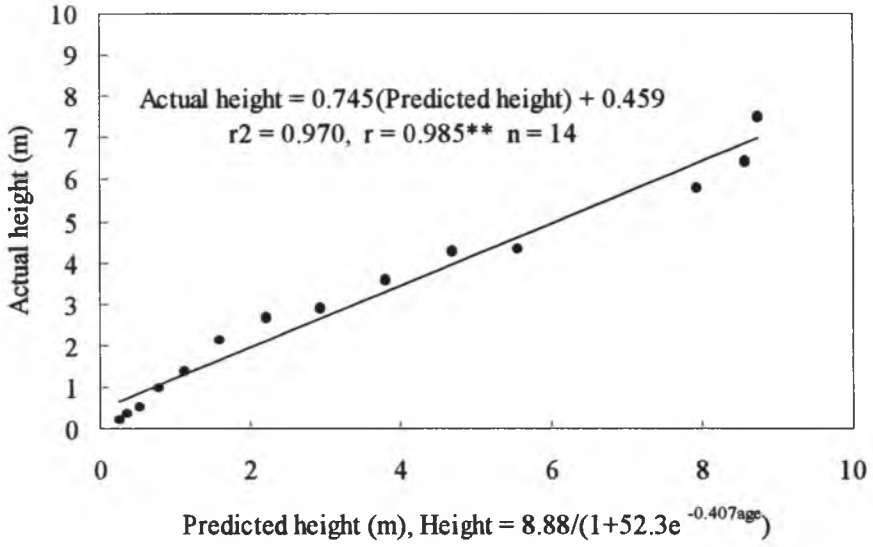

Fig. 2.2 Relationship between actual (means of 20 trees) and predicted height of mangosteen trees in the east coast of Thailand, 1997.

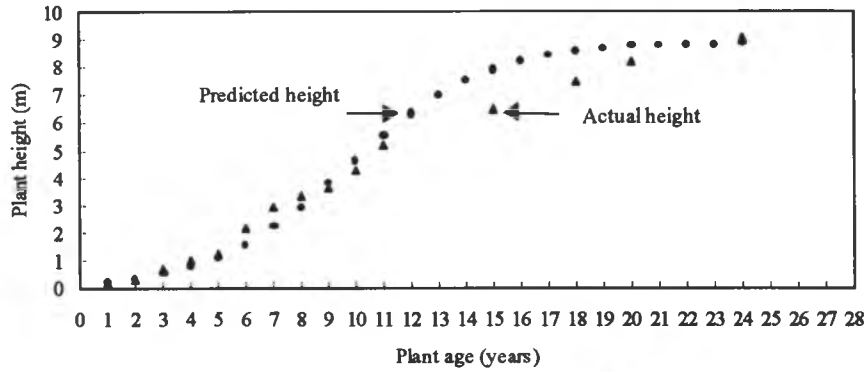

Fig. 2.3 Predicted height, Height = 8.88 / (1+52.3 $e^{-0.407age}$), compared to mean of actual height of mangosteen trees, Chanthaburi, Thailand, 1997.

To determine whether the growth rate of mangosteen trees changed dramatically when a juvenile tree transitioned to the mature phase, the growth rates of the lag, linear, and plateau phase of the growth pattern were compared. Mangosteen seedlings at 1 to 3-years-old and grown in a nursery before transplanting, showed a slope (growth rate) with a linear relationship between height and age of 0.25 meters per year (Fig. 2.4). By comparison, growth rate of mangosteen trees increased to 0.694 meters per year when trees were 5 to 8-years-old, the period from 2 years after transplanting to the first bearing. After bearing, mangosteen developed slowly with a growth rate at 0.457 meters per year (Fig.2.4). Linear relationships of the three growth phases of mangosteen can be presented as :

Growth before transplanting, 1 to 3-year-old (young);

$$\text{A, Height} = 0.25(\text{age}) - 0.117 \quad \ldots\ldots\ldots (2.4)$$
$$r^2 = 0.671, \quad r = 0.819^{**}$$

Growth of near mature mangosteen, 5 to 8-year-old (near mature);

B, Height = 0.695(age) - 2.105 .....(2.5)
r^2 = 0.901, r = 0.949**

Growth of mature mangosteen, after the first bearing (mature);

C, Height = 0.46(age) – 0.393 .....(2.6)
r^2 = 0.956, r = 0.978**

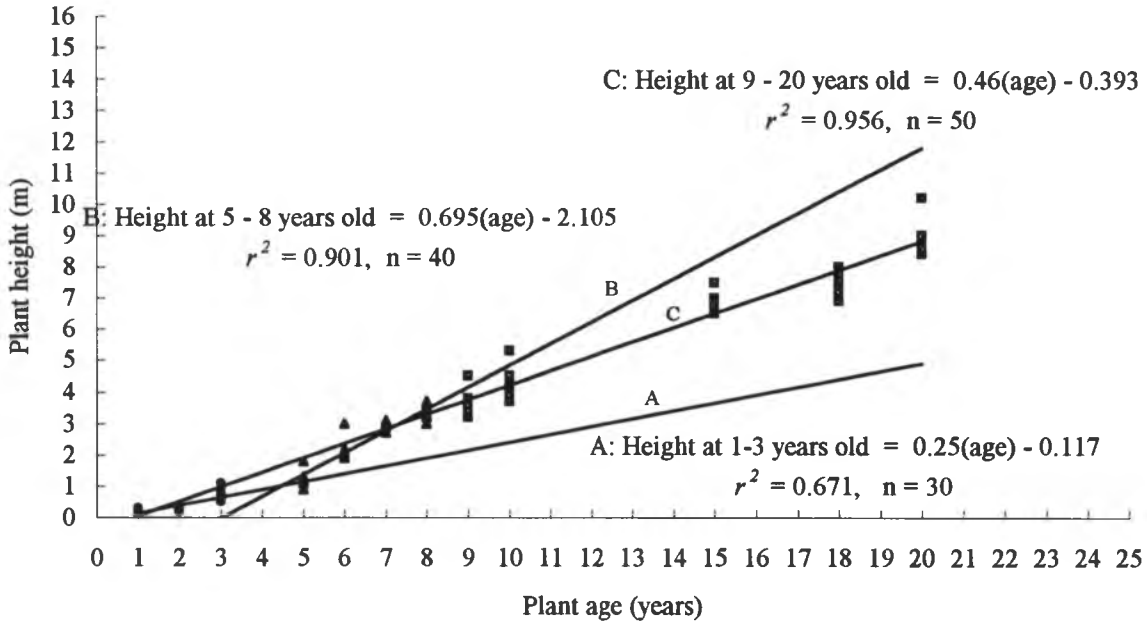

Fig. 2.4 Growth rate of juvenile (line A) and near mature (line B) phase compared to that of mature phase (line C).

When the regression lines are compared they can differ in slope, in y-intercept, and/or in the residual variances. A comparison of the residual variances, followed by the slopes and the y-intercept can then be attempted. Since the standard deviations of untransformed height data of 3 different growth phases were proportional to the means,

the actual height was logarithmically transformed before the comparisons were made (Little and Hills, 1978; Snedecor and Cochran, 1980). After transformation, two regression lines (Fig. 2.4, lines A and B), growth of young mangosteen before transplanting and of near mature trees were compared. The comparison revealed that the growth rates of young and near mature were significantly different (Appendix A, Table A1). Similarly, comparisons of growth rates of near mature to mature mangosteen (Fig. 2.4, line B and C), and of young to mature mangosteen (Fig. 2.4, line A and C) showed significantly different growth rates among those growth phases (Appendix A, Table A2 and A3). These results indicate that the growth rate of the different phases in mangosteen trees were significantly different and can be used to distinguish between each phase (young, near mature, and mature) of development.

2.4 Discussion

To fit the growth pattern of mangosteen trees from seeding to the mature phase, a classical technique using a continuous function was employed. Mean values of actual heights of mangosteen trees at different ages from seeding to 24-years-old were calculated and plotted against plant age. In general, the typical growth curve of any one crop usually follows an approximately S - shaped or sigmoidal pattern and consists of three phases (Milthrope and Moorby, 1979; Richards, 1969). The first phase, an initial lag phase, is characterized by a period of slow but gradually increasing growth rate. During the second period, growth is approximately linear. Finally, at the plateau phase the growth rate declines until the height, length, or any other dimensional parameter reaches

an asymptotic maximum. Cumulative height of 1 to 5-year-old mangosteen trees could be described by an exponential function which showed an initial lag phase between 1 to 3 years from seeding, and when plants were grown in the nursery under controlled conditions in 5.6 liter black polyethylene bags under a shade house covered with 50% black shadecloth (Fig. 2.1). After three years of growth under controlled conditions, mangosteen is normally transplanted to the field and requires approximately two years to adapt to field conditions. Mangosteen growth then dramatically increases under favorable field conditions. A linear growth phase occurred from six years after seeding (Fig. 2.1). Since canopy size of 24-year-old mangosteen trees grown in the Chanthaburi Horticultural Research Center, Department of Agriculture was controlled by topping the trees every 2 years, 8.88 meters was the maximum height, and a plateau phase began at 19 years old. To categorize overall growth, it was advantageous to express the growth by a continuous function. This can provide a conceptual picture of the main features of growth. A continuous function can extract trends and ignore the short-term or minor fluctuations. The polynomial group, $y = a + bx + cx^2 + dx^3 + \ldots$, and a simple logistic relationship, $y = a/(1+be^{-cx})$, based on exponential ($y = ae^{cx}$, $c>o$) and allometric ($y = ax^b$) equations, were the two families of functions that proved useful (Milthrope and Moorby, 1979).

In the early stages of seedling growth, which can last several years in forest trees, shoot growth is rapid and total dry weight of the tree increases exponentially. As the growth rate declines there are associated changes in the morphology of the shoot (Moorby

and Wareing, 1963). These changes reflect an increase in complexity of the shoot. A reduction in dry matter partitioning to various vegetative organs (shoots, branches, stems, leaves, trunk, and roots) can occur due to actively developing reproductive organs (flowers and fruits) in species such as, apples (Heim et al., 1979; Webster and Brown, 1980), citrus (Sanz et al., 1987), strawberries (Schaffer et al., 1986), and peach (Chalmers and Ende, 1975). Among developing vegetative organs, roots are considered as weaker sinks than either developing shoots or leaves (Wright, 1989). De Jong and Grossman (1994) compared the model simulations of plant organ growth under various cropping conditions. According to the model roots received all of the residual carbohydrate available after the requirements of the other organs were met. This may be due to the roots being furthest from the leaves, and over long distances there is greater resistance to assimilate flow (Heim et al., 1979). It has been suggested that a major problem in mangosteen cultivation is its extremely slow rate of development due to poor growth of the root system (Almeyda and Martin, 1976; Downton et al., 1990). The usual explanation for the declined rate of growth during the mature or reproductive phase of mangosteen has been that there is a reduction in assimilate partitioning to vegetative organs, especially during the 5 to 6 months of flower and fruit development. Normal growth and development of the root system could be affected severely by reduced dry matter partitioning. Minimal vegetative growth could also occur due to the trees inability to produce new roots to take up water and nutrients.

It is difficult to expect that any commonly used function will provide a full, clear

and biologically satisfying picture of a complex system over a long length of time. Milthrope and Moorby (1979) stated that simplicity and interpretability with imperfection were preferable to imcomprehensible impeccability. The growth pattern of mangosteen trees from seeding, juvenile period, to mature phase could be described by a logistic function (Eq. 2.3 and Fig. 2.1 and 2.3), which was shown to fit the cumulative height data very well. The growth pattern provided a useful description of mangosteen growth. When the data were analysed for a series of discrete functions, linear function could be fitted to three growth stages where lines A, B and C in Fig. 2.4 could be used to describe growth rates during the juvenile, near-mature, and mature phases of mangosteen, respectively. Using this mathematical approach, statistically significant differences between slopes of various growth phases provided evidence to distinguish the transition from one phase to another. The growth rates i.e., slopes of these lines (line A, B, C in Fig. 2.4), were 0.25, 0.69, and 0.46 meters per year, respectively, and were significantly different from each other. It appears that growth rate of mangosteen trees decreased when they are in the mature phase (0.46 meters per year) compared to when they are in the near mature phase(0.69 meters per year). An experiment on larch also showed that growth rate (change in height or canopy diameter) decreased when plants transitioned to the mature phase (Greenwood et al., 1989). Greenwood and Hutchison (1993) concluded that decreased growth rate or growth potential was one mature characteristic in larch and other conifers.

These findingd indicate that the growth rate of the three different growth phases

can be used to distinguish the transition from, juvenile to near-mature, near-mature to mature, and juvenile to mature phase for mangosteen trees. If the growth of young mangosteen trees can be stimulated as rapidly as possible, trees could undergo transition to the near mature and mature phases earlier and the juvenile period might be reduced.

CHAPTER 3

RELATIONSHIP OF PHASE CHANGE OF MANGOSTEEN WITH AGE AND CANOPY SIZE

3.1 Introduction

Woody species characteristically possess a juvenile phase during which an individual lacks the capacity to flower. After the transition to the mature phase, the plant becomes capable of flowering under appropriate inductive conditions (Bernier et al., 1981; Hackett, 1985). In addition, some morphological, developmental, and biochemical parameters such as branch number and branching pattern (Libby and Hood, 1976), shoot growth vigor (Goodin, 1964; Sweet and Wells, 1974), and changes in duration of the plastochron (Stein and Fosket, 1969) are associated with the ability to flower in many species. Visser (1965) showed that apple and pear seedlings attained a certain size before they transitioned to the mature phase. Longman and Wareing (1959), Mullins et al. (1989), Robinson and Wareing (1969), and Zimmermann (1971) also showed that achieving a minimum size may be more important in the juvenile-to-mature transition in *Larix leptolepis*, *Citrus* spp., *Ribes nigrum*, and *Malus hupehensis* than age or number of dormancy cycles. A minimum number of leaves and/or leaf area are also associated with phase change in many herbaceous and woody plants (Bernier et al., 1981; Sussex, 1989; Zimmermann, 1972). It is not only theoretically important to understand the factors which cause and influence prowth patterns but it is also of considerable practical interest to plant scientists, since these factors may be altered to manipulate the juvenile-to-mature

transition of the plant and consequently its breeding cycle.

The previous chapter showed that the growth rate of juvenile, near mature, and mature phases of mangosteen trees can be used as a developmental feature to characterize phase change as trees attain maturity. The following investigation was conducted to investigate the relationship between tree age and tree size and the juvenile-to-mature transition of mangosteen.

3.2 Materials and Methods

Plant material. The study was conducted between 1995 and 1998 in 3 mangosteen orchards in Chanthaburi province and 1 orchard in Trad province, which are situated from Bangkok to the Cambodian border on the east coast of Thailand, between 12-13°N to 101-102°E. The soil type is mainly a sandy loam with a pH of about 5 to 6.5. The average annual rainfall is 3126 $\pm$ 216.9 mm and is distributed over about 6 months. Two hundred trees used in the study were 5.5 to 11-years-old, and averaged 3.30 m x 2.88 m (height x width), at the end of study. The trees were grown in full sun and planted on an average spacing of 10 x 10 m. Agro-management practices during vegetative development, flower development, and fruit growth and development in all orchards were based on a recommendation of Chanthaburi Horticultural Research center. Irrigation was applied by either a sprinkler or flooding system and was based on requirements of mangosteen at different stages of development. The requirements at vegetative growth, flower development, and fruit development were 60%, 75%, and 80% of the daily evaporation from a class A evaporation pan, respectively (Poonnachit et al., 1992).

Granular fertilizers, 16N-16P_2O_5-16K_2O, 8N-24P_2O_5-24K_2O, and 13N-13P_2O_5-21K_2O were applied about 1.5 kg each per tree to the soil immediately after harvest, 2 to 3 months later, and during fruit growth and development, respectively.

Measurements :

Height and canopy diameter in meters for 200 mangosteen trees were measured annually at flowering time. Tree height measurements were made from the top to the base of the canopy. Canopy diameter at its maximum point was also measured. Canopy size of all trees was calculated from height and canopy diameter data. Since canopy of mangosteen trees are approximately cylindrical in shape and fruits have a tendency to be produced at the perimeter of the canopy, canopy area (m^2) of mangosteen trees was calculated based on the surface area of a cylinder. The formula to calculate the surface area of trees was $2\pi(d/2)^2 + \pi dh$, where d and h were canopy diameter and height in meters, respectively. The number of years that trees produced at least 10 flowers per tree during 3 consecutive years of observation (1995-1998) was recorded and expressed as the number of flowering years for each tree age and each canopy area.

Statistical analysis :

Regression relationships between the number of flowering years and canopy area and age were calculated. Multiple regressions between number of flowering years and canopy area and age were also computed to examine whether canopy area and/or age were associated with the juvenile-to-mature transition.

3.3 Results

The relationship between number of flowering years and canopy area of mangosteen trees was linear with a regression coefficient (slope) of 0.031 (Fig.3.1). The correlation was strong, giving an r^2 of 0.71 (n = 200). Based on the above relationship it could be estimated that the first bearing of mangosteen trees occurred when their surface canopy area was 50.3 m^2. Since the canopy area increased relative to age under constant favorable growing conditions (Fig. 3.2), a regression between number of flowering years and age was obtained. The relationship between number of flowering years and age gave an r^2 of 0.43 (n = 200) (Fig. 3.3), and estimated that mangosteen trees started to attain the ability to flower when they were 7.9 years old after seeding. When effects of both canopy area and age on number of flowering years were combined by a multiple linear regression (Number of flowering years = 0.036(canopy area) – 0.075(age) – 0.235, r^2 = 825**), canopy area had greater contribution to precocity than age, because its standard regression coefficient (0.958) was greater than that of age (0.11) (Appendix B).

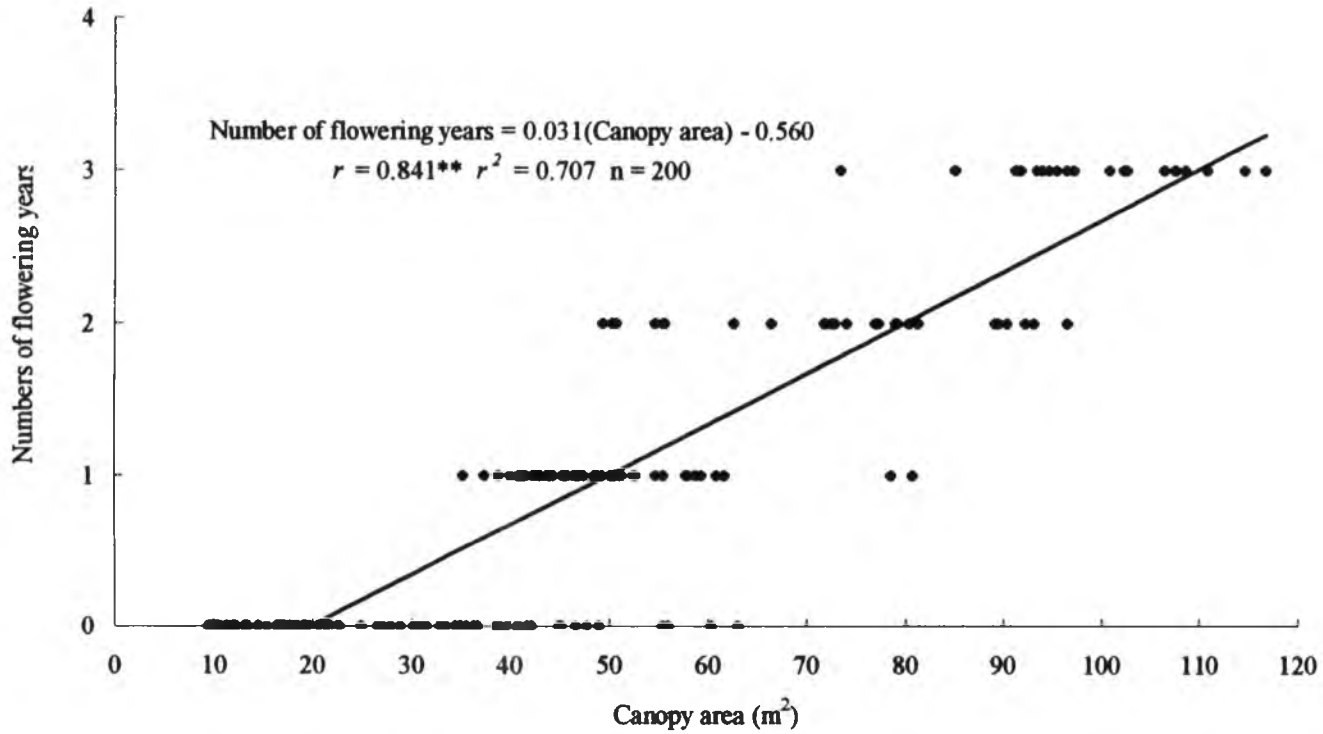

Fig. 3.1 Numbers of years that mangosteen trees flowered during 3 consecutive years of observation as a linear function of canopy area (m^2). Each point represents one tree. Data were collected from 4 different locations along the east coast of Thailand.

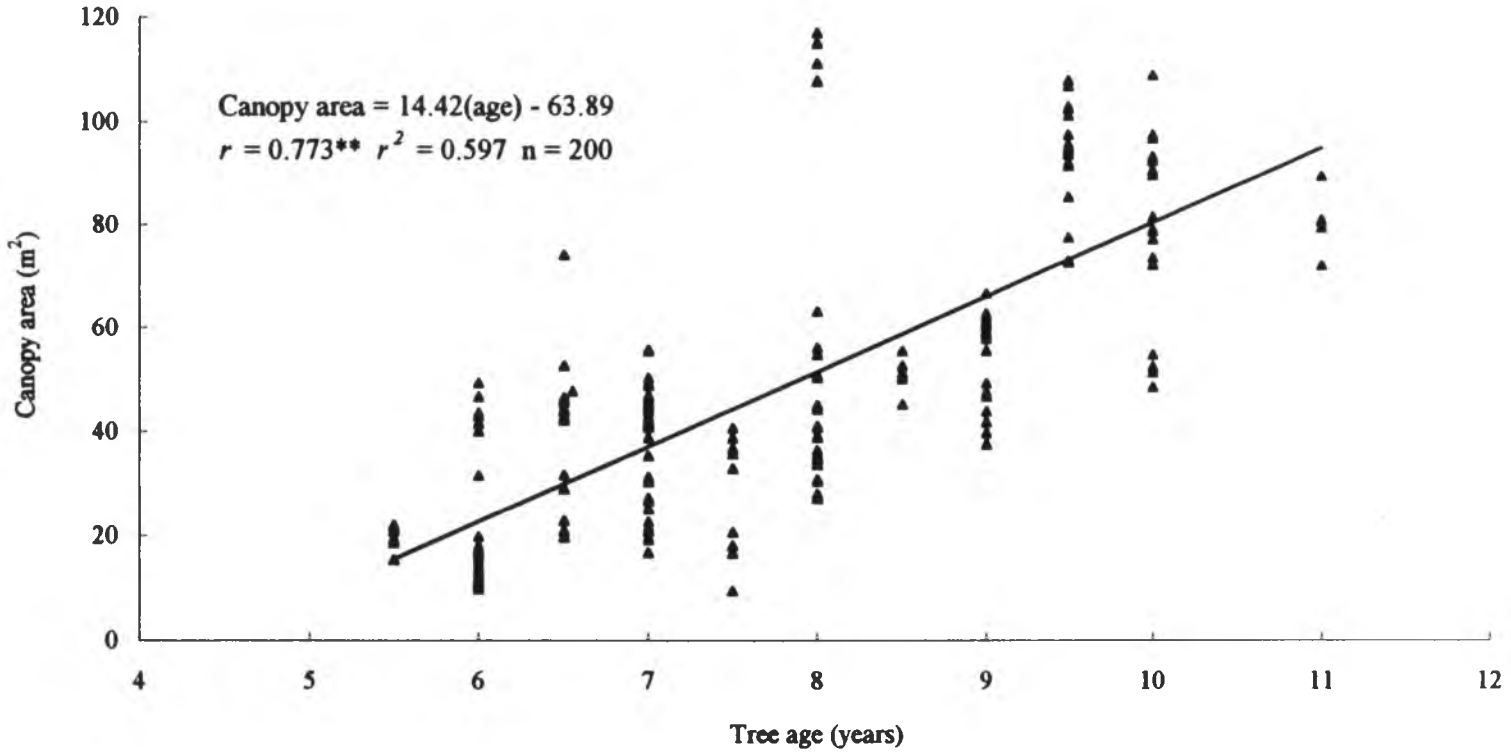

Fig. 3.2 Relationship between canopy area (m^2) of mangosteen tree with tree age between 5.5 to 11 years old as a linear function of plant age (years). Each point represents one tree. Data were collected from 4 locations along the east coast of Thailand.

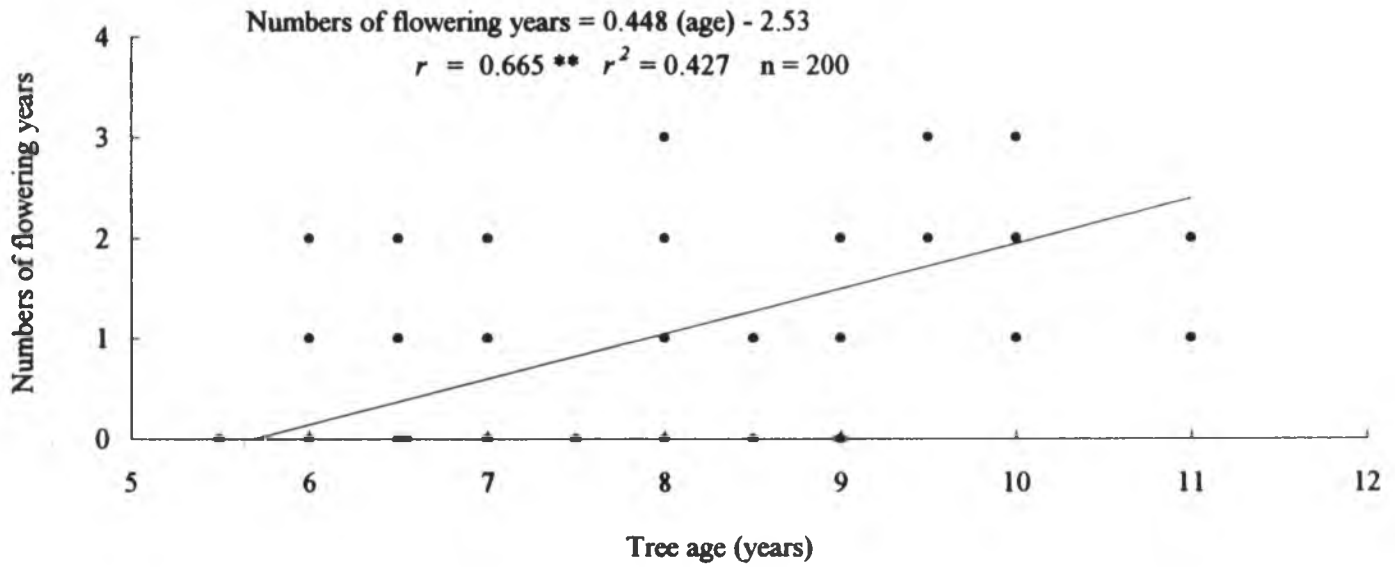

Fig. 3.3 Numbers of years that mangosteen trees flowered during the 3 consecutive years of observation as a linear functio tree age. Each point represents one tree. Data were collected from 4 locations along the east coast of Thailand.

3.4 Discussion

It has been widely accepted that mangosteen exhibits a long juvenile period when trees are grown from seeds. Trees require from 10 to 15 years to first flowering, or until 32 primary branches are laterally produced (Moncur, 1988; N. Ponchua, personal communication). The estimated age of 7.9-years-old, that was derived from a positive regression between numbers of flowering years and age in Fig. 3.3 confirmed the observations of Moncur (1988) and N. Ponchua (personal communication). Since the canopy area and age of mangosteen were strongly correlated as shown in Fig. 3.2, the relationship between numbers of flowering years and canopy area could be expected. The canopy area was correlated with numbers of flowering years, giving a high r^2 of 0.71 compared to age which was $r^2 = 0.43$. When the effects of canopy area and age on numbers of flowering years were combined, canopy area had a larger standard regression coefficient (0.985) than age (0.11) indicating that canopy size had more of an effect on precocity of mangosteen than age. It also implied that the sooner trees attained the appropriate size, the earlier the precocity. The investigation in mangosteen agreed with the phase change studies in *Ribes nigrum* L. (Robinson and Wareing, 1969), *Malus hupenhensis* (Zimmermann, 1971), *Citrus aurantifolia* (Christm.) Swing., *C. paradisi* Macf., and *Fortunella* sp. x *C. reticulata* Blanco hybrid (Snowball et al., 1988), and *Pinus* spp. (Greenwood, 1995; Greenwood and Hutchison, 1993) which proposed that achieving a minimum size was more important in the phase change than age.

The investigation on mangosteen tree growth, and related characteristics to

distinguish its phase change indicated that the juvenile-to-mature transition of mangosteen trees was associated with not only the differences in the growth rate between different growth phases, but also the attainment of a certain minimum canopy size.

It is not known why attainment of a minimum size is required for the transition to the mature phase. Snowball et al. (1988) suggested that plants must attain a certain size and/or age before they were competent to response to internal or external floral stimuli. Visser (1973) indicated that roots and/or proximity to roots may be involved. Frydman and Wareing (1973) also suggested that the juvenile phase was maintained because of the proximity of the shoot apex to roots, which produce high levels of gibberellins. Several results in English ivy (Hillaman et al., 1974; Rogler and Hackett, 1975) and eucalyptus (Paton et al., 1970) indicated that endogenous inhibitors were involved in phase characteristics. There is also other evidence suggesting that substrate availability may be important in phase change. For example low light intensity and high temperature which can reduce carbohydrate levels, prolonged the juvenile phase in English ivy and *Acacia melanoxylon* R. Br., *Fagus sylvatica* L., and *Rubus idaeus* L. (Rogler and Hackett 1975). Allsopp (1968) suggested that assimilate buildup caused stable alterations of apical activity which were observed in the transition to the mature phase. Thus, the correlation between the attainment of a certain size and the transition to the mature condition in some instances can be explained via the involvement of growth regulators and assimilate factors. Increases in size can alter the shoot apex position relative to other plant parts. This could then influence how sources of photosynthates, hormones, and water interact with various

meristems involved in flowering.

CHAPTER 4

PHOTOSYNTHETIC CHARACTERISTICS OF MANGOSTEEN LEAVES

4.1 Introduction

The light environment in which leaves of various plant species develop influences their morphology, anatomy, and physiology (Bazzaz and Carlson, 1982; Campbell et al., 1992; Hampson et al., 1966; Syvertsen and Smith, 1984; Wiebel et al., 1994). Natural shading within a canopy results in anatomically distinct leaves with differing gas exchange characteristics (Campbell et al., 1992; Hampson et al., 1996; Kappel and Flore, 1983; Schaffer and Gaye, 1989; Syvertsen, 1984; Syvertsen and Smith, 1984). Information on the photosynthetic characteristics of the leaves of mature mangosteen trees grown in full sun is very limited. Previous studies (Wiebel et al., 1993, 1994) provided information on gas exchange characteristics of 2-year-old mangosteen seedlings maintained in shade houses that transmitted a maximum photosynthetic photon flux density (PPFD) of 250, 800, and 1400 μmol m^{-2} s^{-1} and in full sun. The maximal photosynthetic rates ($P_{n\ (max)}$) ranged from 3.7 to 4.1 μmol m^{-2} s^{-1} with on significant difference among seedlings grown in the different shade treatments despite significantly different morphologies. Light saturation for leaves grown in 20% shade (1400 μmol m^{-2} s^{-1}) was higher (951 μmol m^{-2} s^{-1}) than leaves grown in 50% (800 μmol m^{-2} s^{-1}) and 80% shade (250 μmol m^{-2} s^{-1}) (645 and 555 μmol m^{-2} s^{-1}, respectively) whereas light compensation points (9-15 μmol m^{-2} s^{-1}) and quantum efficiencies (0.022-0.023 mol mol^{-1}) did not differ significantly among the shade treatments. Since light levels for leaves at different positions within the canopy

grown in full sun are not constant, photosynthetic response of the mature trees to diurnal light levels is of interest.

The objective of this study was to determine the photosynthetic and leaf characteristics of mature mangosteen trees grown in full sun. These characteristics can provide baseline information that may be important in understanding mature tree physiology and in future studies on canopy management practices.

4.2 Materials and Methods

Plant material. Ten 23-year-old mangosteen trees grown in full sun on the Chanthaburi Horticultural Research Center research plot, Chanthaburi, Thailand, were used. The photosynthetic rate (P_n) of fully mature leaves were measured and their leaf characteristics were determined over different levels of PPFD in the canopy. Trees were planted at 8 x 8 m spacing (156 trees/ha) and had an average height and width (canopy diameter at its maximum point) of 8.5 and 7.6 m, respectively. The trees were irrigated by a sprinkler system with the following fractions of the daily 1.20 m diameter pan evaporation: during vegetative development, 0.6; during flower development, 0.75; and during fruit development, 0.8 (Poonnachit et al., 1992). Fertilization per tree included 2.5 kg 16N-16P_2O_5-16K_2O applied immediately after harvest, 2.5 kg 8N-24P_2O_5-24K_2O applied about 2-3 months later, and 2.5 kg 13N-13P_2O_5-21K_2O applied about 1 month after anthesis.

Measurements :

Net photosynthetic rate (P_n) was measured for 1 to 2 hours near midday on clear days. All measurements were made on single attached fully mature leaves (6 replicates) of the terminal flush positioned at the interior, exterior, top, and base of the canopy where PPFD levels were different. Measurements were made on two mangosteen trees with a portable photosynthesis system (LI 6200, Li-Cor, Lincoln, Nebraska, USA) equipped with a 1-liter chamber. P_n rate and stomatal conductance (g_s) were also measured on single fully mature leaves of the terminal flush on 3 mature trees at hourly intervals (06:00 to 14:00 hour on clear days). These data represented the photosynthetic characteristics of mature leaves grown in full sun. Both measurements were made in November 1998 (the cool dry season) when the average maximum/minimum temperatures on days of measurement were 32.3°/23.5°C.

Leaf length and width at the broadest part of fully mature leaves (5 replicates) from the top, base, exterior, and interior of the canopy were measured on 5 mangosteen trees. Incident PPFD was also recorded between 11:00 and 13:00 hour at the time leaf dimension data were collected was taken using a point quantum sensor (LI 190SA) equipped with a data logger (LI 1000, Li-Cor, Lincoln, Nebraska, USA). Leaf areas were then calculated from the formula; LA = 0.699 (W*L) + 4.674, r^2 = 0.994 where LA = leaf area in cm^2, W the maximum leaf width and L the leaf length in cm (S. Salakpetch and S. Chandraparnik, unpublished 1996). The leaves were subsequently oven dried at 65°C for 72 hours to determine dry weight. Specific leaf area (SLA, $cm^2\ g^{-1}$) was also calculated from leaf area and leaf dry mass. The investigation was made in November 1998 (the cool

dry season), 1 month before the trees flowered. The measurement was made on 5 mangosteen trees.

Data analysis :

Photosynthesis (P_n) data for fully exposed mature leaves measured throughout the day as PPFD varied and of P_n of mature leaves grown at different levels of PPFD within and outside the canopy were plotted against PPFD. The P_n data of mature leaves exposed to full sun was fit to a negative exponential (monomolecular) function. The function used was based on McArthur-Wilson equilibrium equations as described by Campbell et al. (1992), as dark respiration was expected to be negative. The negative exponential equation was:

$$P_n = S\,(1 - e^{-G*PPFD}) \quad \ldots(4.1)$$

where P_n = net photosynthetic rate (μmol CO_2 m^{-2} s^{-1})
S = asymptotic maximum P_n rate
e = base of natural logarithm
G = rate of approach to the maximum
PPFD = photosynthetic photon flux density (μmol m^{-2} s^{-1})

Quantum efficiency, mol CO_2 fixed per mol quanta absorbed, was estimated from initial slope of the P_n-light response curve for exposed leaves and by linear regression over the range of PPFD between 0 to 100 μmol m^{-2} s^{-1}. No adjustment was made for dark respiration.

Light saturation point, the PPFD that resulted in 95% of maximal photosynthetic rate ($P_{n\,(max)}$), was also interpolated from equation 4.1.

Light compensation point (gross photosynthesis just balances respiration) could not be estimated due to the limitation of the exponential equation.

Leaf dry weight and SLA also were plotted against PPFD for leaves located at different positions within the canopy.

4.3 Results

The P_n rate of mature leaves exposed to full sun increased rapidly with increasing PPFD between 0 and 200 μmol m^{-2} s^{-1}, followed by a gradual leveling of P_n rate between 200 and 600 μmol m^{-2} s^{-1} before reaching a plateau (Fig. 4.1). Light saturation occurred at about 600 μmol m^{-2} s^{-1}, which represented about 30% of typical full sun values of 2000 μmol m^{-2} s^{-1} of PAR (Nobel, 1983). The P_n rate of fully mature mangosteen leaves exposed to full sun in response to PPFD was well fitted by the negative exponential function with an r^2 of 0.98 (Fig. 4.1). The light compensation point estimated from the photosynthetic response curve was 10.2 μmol m^{-2} s^{-1}. The quantum efficiency estimated from the initial slope of the P_n equation was 8.522 x 0.0038 = 0.032. The slope of the regression line between P_n and PPFD over the range 0 to 100 μmol m^{-2} s^{-1} (P_n = 0.98 + 0.029(PPFD), r^2 = 0.974) gave an quantum efficiency of 0.029 mol CO_2 fixed per mol quanta absorbed, the average for both methods, was 0.03 mol mol^{-1} (Table 4.1).

Table 4.1 Gas exchange characteristics of fully mature leaves of mangosteen grown in full sun at the Chanthaburi Horticultural Research Center.

Max. photosynthetic rate (μmol CO_2 m^{-2} s^{-1})	8.5
Light (PPFD) compensation point (μmol photon m^{-2} s^{-1})	10.2
Light saturation point (μmol photon m^{-2} s^{-1})	600
Quantum efficiency (CO_2 fixed / quanta absorbed; mol mol^{-1})	0.03

The P_n response of mature leaves of the terminal flushes located at different levels of PPFD within the canopy was similar to, but generally less than, that of exposed leaves (Fig. 4.1). P_n rate of shade leaves located inside the canopy which had PPFD of about 15 to 200 μmol m^{-2} s^{-1} at the time of measurement was lower (from 0.9 to 5.1 μmol m^{-2} s^{-1}) than rates for sun grown leaves on the same tree (Fig. 4.1).

The g_s of mature mangosteen leaves exposed to full sun increased rapidly with increasing PPFD between 0 and 600 μmol m^{-2} s^{-1}, and then more gradually beyond PPFD of 600 μmol m^{-2} s^{-1} before reaching an maximum g_s (about 450 mmol m^{-2} s^{-1}) at PPFD of about 900 μmol m^{-2} s^{-1} (Fig. 4.2). At PPFD higher than 900 μmol m^{-2} s^{-1}, g_s decreased whereas the P_n rate remained constant (Fig. 4.1).

The total dry weight of fully mature leaves at different levels of PPFD within the canopy increased from 1,173 to 2,044 mg for leaves located within the canopy where the PPFD at midday was between 6.5 and 27.7 μmol m^{-2} s^{-1} (Fig. 4.3). Dry weight decreased progressively and quite rapidly to 1,149.4 mg as midday PPFD increased from 27.7 to 504

μmol m^{-2} s^{-1}. At midday PPFDs above 504 μmol m^{-2} s^{-1}, leaf weight continued to decrease gradually. PPFD values between 6.5 and 200 μmol m^{-2} s^{-1} were measured inside the canopy, whereas those above 200 μmol m^{-2} s^{-1} were measured when leaves were exposed to full sun at the top and exterior of the canopy. Changes in leaf areas of mature leaves at different levels of PPFD in the canopy were similar to that of the leaf dry weight since there was a close relationship between leaf dry weight and leaf area (Leaf dry weight (mg) = 347.67 + 83943.33 (LA, m^2), r = 0.908** n = 10).

The SLA, describes leaf area ratio in terms of leaf thickness, at different levels of PPFD in the canopy ranged from about 81 to 99.5 cm^2 g^{-1} where midday PPFD was between 6.5 and 27.7 μmol m^{-2} s^{-1} (Fig. 4.4). SLA of shade leaves inside the canopy decreased to about 78.2 cm^2 g^{-1} as midday PPFD increased from 27.7 to 515.7 μmol m^{-2} s^{-1}. At midday PPFDs above 515.7 μmol m^{-2} s^{-1}, SLA continued to decrease to about 46.8 cm^2 g^{-1} where PPFD was 1752 μmol m^{-2} s^{-1} (Fig. 4.4).

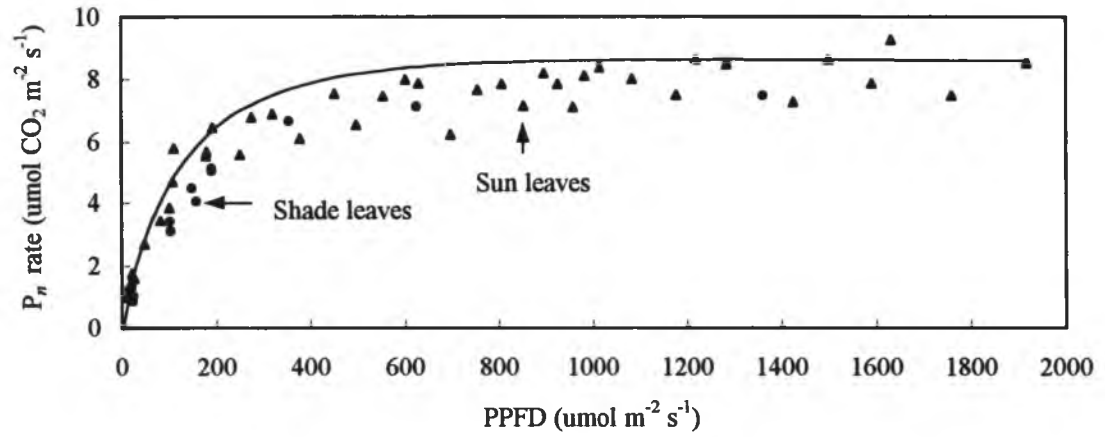

Fig. 4.1 Scatter plot of observed photosynthetic rate (P_n) of fully mature leaves at different positions in the tree canopy and of exposed leaves to full sun. The data were well fitted by the negative exponential model for exposed leaves to full sun ($P_n = 8.522\ (1\text{-}e^{-0.0038PPFD})$), $r^2 = 0.98$, n = 16, P_n = photosynthetic rate, PPFD = photosynthetically photon flux density. Each data point represents the mean of 6 leaves.

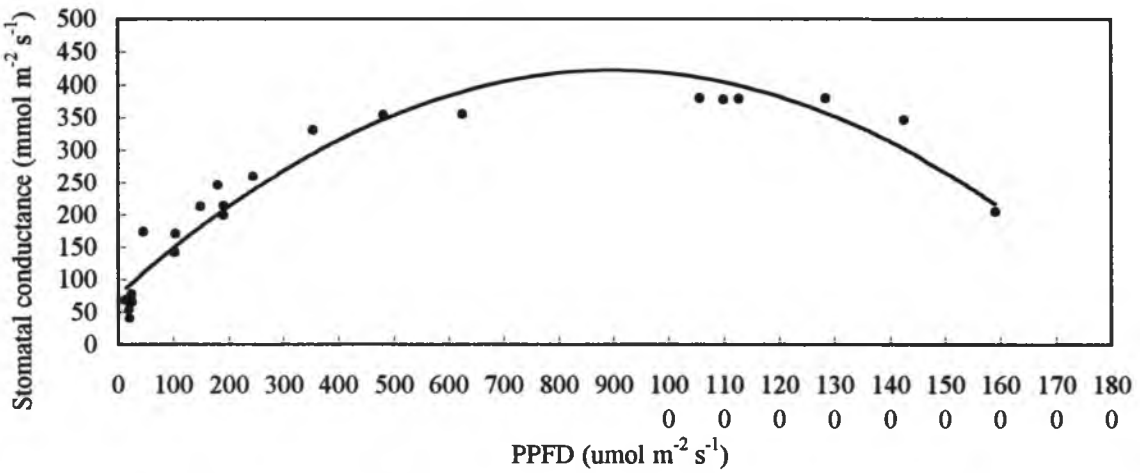

Fig. 4.2 Stomatal conductance (g_s) of fully mature mangosteen leaves exposed to full sun. Each data point represents the mean of 6 leaves.

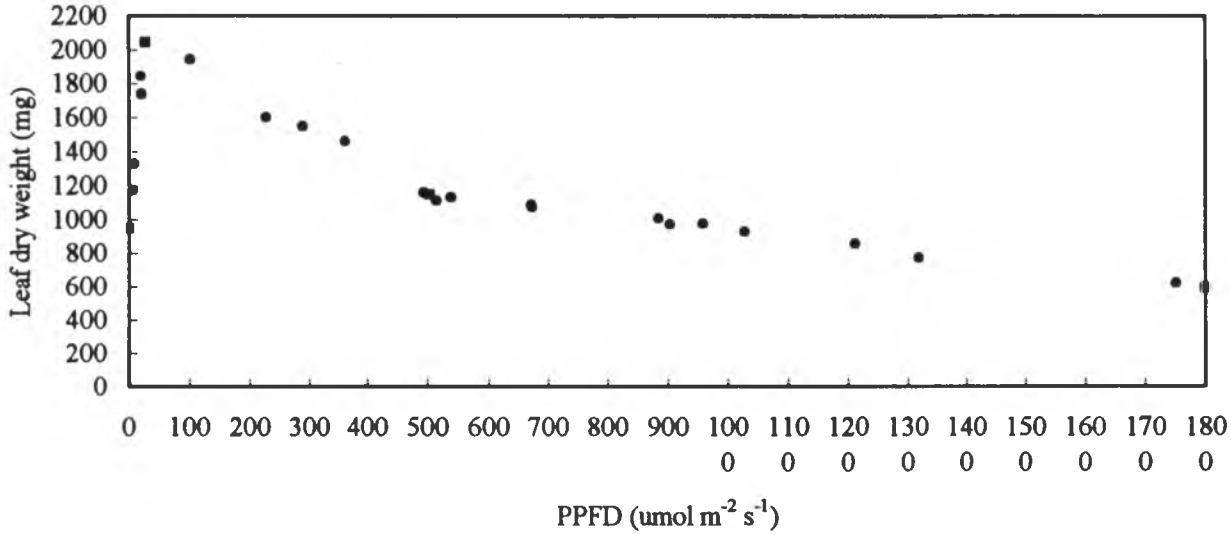

Fig. 4.3 Dry weight of fully mature mangosteen leaves grown in response to PPFD at different levels in the canopy. The measurement was taken between 11:00 and 13:00 hour on full-sun days.

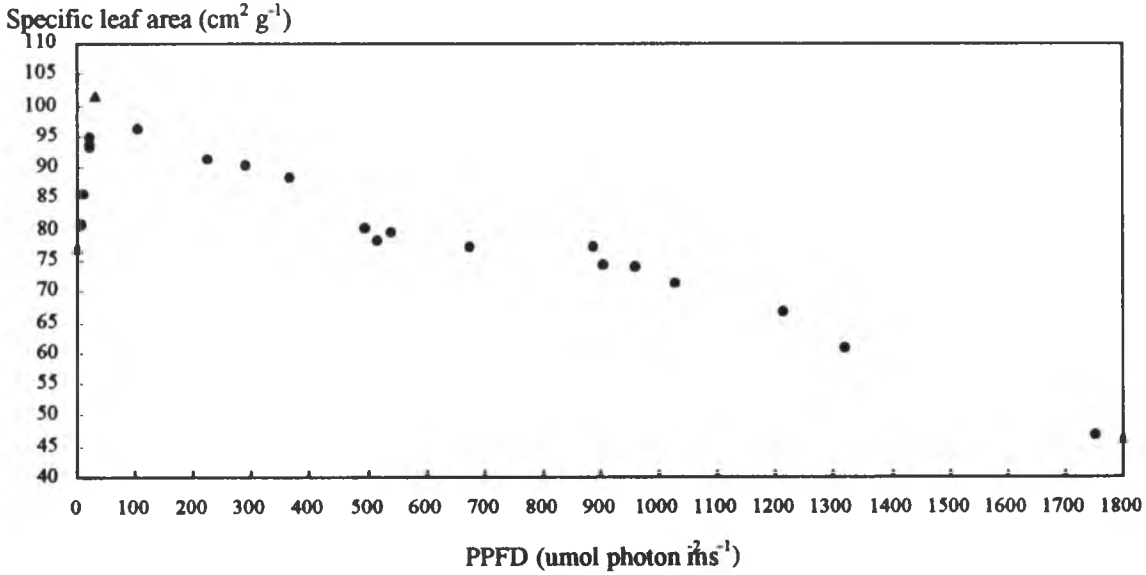

Fig. 4.4 Change in specific leaf area of fully mature mangosteen leaves in relation to PPFD measured near midday at various positions in the canopy, Chanthaburi, Thailand.

4.4 Discussion

While the photosynthetic rate of fully mature mangosteen leaves in response to light (Fig. 4.1) was similar to that described for several other crops, leaves exhibited lower $P_{n(max)}$ than 'Delicious' apple (Campbell et al., 1992), hazelnut (Hampson et al., 1996), and 'Duncan' grapefruit (Syvertsen, 1984), which had $P_{n(max)}$ values of about 10 to 14 μmol m^{-2} s^{-1} in full sun. The $P_{n(max)}$ (8.5 μmol m^{-2} s^{-1}) for sun-grown mangosteen leaves was about twice the rate obtained for mangosteen seedlings grown in shade (Wiebel et al., 1993) and several rainforest tree seedlings (Langenheim et al., 1984), but similar to 'Pineapple' orange (Syvertsen, 1984), satsuma mandarin (*Citrus unshiu* Marc.) and Ponkan (*C. reticulata* Blanco.) (Morinaka, 1992). The lower P_n rate of mangosteen seedlings grown under shade treatments when compared to sun-grown mature trees may help to account for the slow growth rate of the young mangosteen seedlings.

The photosynthetic light response curve (Fig. 4.1) was well fitted by the MacArthur-Wilson equilibrium equations (Campbell et al., 1992) and could be used to estimate the P_n rate of mangosteen trees grown in full sun in well-managed conditions. The equations were more advantageous than quadratic equations because they lack the decrease in P_n with higher PPFD, a calculation artifact associated with use of the quadratic equation. The parameters in the equation also allowed the statistical comparisons of the entire light response curve to determine whether two light response curves differed from each other. However, an inherent disadvantage of this equation is that the light compensation point cannot be determined.

Vu and Yelenosky (1988) determined that PPFD values between 600 and 1000 μmol m^{-2} s^{-1} was about the saturation level for RuBP carboxylase of 'Valencia' orange leaves. Also, the PPFD at light saturation of P_n in'Valancia' leaves occurred at PPFDs between about 600 to 800 μmol m^{-2} s^{-1}. They further suggested that the response observed in citrus may be typical of other horticultural and forest tree species. The P_n data for mangosteen are consistent with this observation. Hampson et al. (1996) and Higgins et al. (1992) reported that the light compensation point for hazelnut, pome fruits, and almond was between 28 and 67 μmol m^{-2} s^{-1}. The light compensation point of 10.2 μmol m^{-2} s^{-1} for mangosteen leaves (Table 4.1) was in agreement with the data of Wiebel et al. (1993) who obtained a value of 9.2 μmol m^{-2} s^{-1} for leaves grown in 80% shade (250 μmol m^{-2} s^{-1} PPFD), and was similar to values (8-16 μmol m^{-2} s^{-1}) for other C_3 plants (Nobel, 1999), but was lower than hazelnut, pome fruits, and almond.

Wiebel et al. (1993) determined that the quantum efficiency for mangosteen leaves in 80%, 50%, and 20% shade treatments did not differ and corresponded to about 0.022 mol CO_2 fixed mol quanta absorbed^{-1} or about 45 quanta per mol CO_2 fixed. Although, there have been reports that plants of the same species grown in shade typically had higher quantum efficiency than their counterparts grown in sunlight (Ehleringer and Pearcy, 1983; Langenheim et al., 1984; Syvertsen, 1984), the result of this study shows that higher quantum efficiency was obtained on leaves of field-grown mangosteen trees (33 quanta per mol CO_2 fixed) compared to that of shade-grown potted seedlings. The stomatal conductance (g_s) for mature leaves of sun-grown mangosteen trees at light saturation in the present study (about 390 mmol m^{-2} s^{-1}) was also higher than that of the shade-grown

seedlings (about 100-125 mmol m^{-2} s^{-1}) (Wiebel et al., 1993, 1994). The higher g_s in this study is consistent with the higher P_n values that were observed for sun-grown mangosteen leaves. Limited volume in pots could result in nutrient and/or water stress conditions which may be the cause of the low rates of g_s of the shade-grown seedlings (Wiebel et al., 1993, 1994). The reciprocal of quantum efficiency, the quantum requirement per CO_2 consumed has a theoretical minimum of 8 to 12 quanta, and of 19.23 quanta, on average, for other C_3 species (Ehleringer and Pearcy, 1983). The quantum requirement reported for hazelnut, which is anunderstory tree in its native forest habitat of Europe (Kull and Niinemets, 1993), was about 23 (Hampson et al., 1996). Based on the data obtained in this study mangosteen, a native understory to the Malay Archipelago (Moncur, 1988), appears to have a higher quantum requirement than hazelnut.

The photosynthetic characteristics, light compensation point, light saturation, and maximal P_n rate of leaves of shade-grown plants generally are lower than those of their counterparts grown in full sun (Bjorkman, 1981; Boardman, 1977; Friend, 1984; Langenheim et al., 1984; Schaffer and Gaye, 1989). Such was the case in this study (Fig. 4.1), though results were only about 10-30% less at any given PPFD. Chalmers et al. (1975), Fails et al. (1982), Kappel and Flore (1983), Syvertsen (1984), and Schaffer and Gaye (1989) found that P_n rates throughout the peach, *Ficus benjamina* L., citrus, and mango canopies were different.

In the present study, leaves located inside the canopy were larger and thinner than leaves located at the outer edge of the canopy. However, in the interior of the canopy

where midday irradiance values were extremely low both leaf area and leaf dry weight increased dramatically (Fig. 4.3). Wiebel et al. (1994) also reported that with higher shade levels, mangosteen seedlings had increased average leaf size but reduced number of cell layer and cell size in the palisade and spongy mesophyll, resulting in thinner leaves. The larger and thinner leaves observed in the present study may be due to the morphological adaptation which is commonly observed when leaves grown at lower irradiance (Boardman, 1977; Corre, 1983; Givnish, 1988). Although the leaf is an integrator of available PPFD, which is almost never constant in a canopy, mangosteen leaves growing inside the canopy would receive lower levels of PPFD than leaves growing at the top or the exterior of the canopy. Mangosteen leaves growing inside the canopy would be expected to have a lower maximum P_n rate, larger size and higher SLA than leaves exposed to full sun on the same tree. The higher total dry weight of leaves in the interior of the canopy apparently results from the fact that area increases more rapidly than leaf dry weight decreases in deep shade. Such results are not common.

The low P_n and g_s, and leaf anatomy and morphology observed in leaves of field- and shade-grown potted mangosteen seedlings (Wiebel et al., 1993, 1994) indicate that mangosteen seedlings has photosynthetic and leaf characteristics associated with shade-tolerant understory trees. Since mangosteen leaves of the mature trees and of the seedlings grown in 50% or 20% shade had higher PPFD saturation point and g_s than seedlings grown in deeper shade, the data indicated that mangosteen leaves can adapt to sun-grown conditions. Thus, it is predicted that gradually and early adaptation trees to full sun should increase growth rate of mangosteen seedlings.

CHAPTER 5

METHODS TO ACCELERATE GROWTH OF JUVENILE MANGOSTEEN

5.1 Introduction

Earlier findings in the present study have shown that the growth rates of mangosteen seedlings are extremely slow during the first 3 years after seeding, but increase rapidly between the 5th and 8th year. Enhancing the growth rate of seedlings grown under optimal growing conditions, by breaking bud dormancy, may offer a promising approach to attaining more rapid size increases in young plants. The outcome could be a reduction in the juvenile period.

Wiebel et al. (1992) reported on the influence of gibberellins A_3, A_4, A_{4+7}, 6-benzyladenine (BA), naphthalene acetic acid (NAA), and GA_{4+7}+BA on bud dormancy and growth of mangosteen seedlings. Their results showed that GA_3, GA_4, and GA_{4+7} were effective in overcoming bud dormancy of the seedlings only when applied directly to the buds. GA_{4+7}+BA was the most effective plant growth regulator by providing 100% bud-break within a week after application, whereas NAA was ineffective. BA was reportedly effective only when applied to seedlings younger than 1-year-old. Broome and Zimmermann (1976) and Williams and Stahly (1968) showed that BA application could promote growth of dormant buds in crabapple and apple. GA_{4+7} application also increased height of containerized carambola seedlings, which attained graftable size in a shorter period, leading to a more rapid turnaround of inventory (Marler and Mickelbert, 1992). Oliveira and Browning (1993) demonstrated that GA_3, GA_4, GA_7 and GA_1 could enhance

shoot growth of *Prunus avium* seedlings as well as promote terminal shoot growth of mature trees. Runner production in 'Tribute' dayneutral strawberries (*Fragaria* x *ananassa* Duch.) increased linearly with combination sprays of BA and GA_3 (Dale et al., 1996) whereas BA or GA_3 alone increased runner production inconsistently (Kender et al., 1971; Pritts et al., 1986; Reid, 1983). Growth of vegetative and flower buds in 'delicious' apple could be promoted by BA alone or in combination with GA_{4+7} (Shaltout and Unrath, 1983). Thiourea is among the most effective rest-breaking agents and was developed into a commercial spray for peach orchards (Blommaert, 1964, 1965). Thiourea was also reported to intensify the number of inflorescences per unit length of branch when sprayed on branches of durian trees at the stage when flower buds could be detected (Chandraparnik et al., 1992). Erez et al. (1971) reported that potassium nitrate and cytokinin also advanced flower bud opening while thiourea had a more pronounced effect on leaf bud opening in peach, plum, apricot, apple, and grapevines. A concentration of 20000 mg l^{-1} thiourea was too high and damaged flower buds, leaf buds, and young shoots (Erez, 1975). Wolak and Couvillon (1977) demonstrated leaf phytotoxicity in peach trees 1 week following application of 5000 or 10000 mg l^{-1} thiourea + 20000 mg l^{-1} potassium nitrate. Poonnachit et al. (1996) succeeded in promoting synchronized leaf flush and reducing phytotoxicity following 2500 mg l^{-1} thiourea + 30000 mg l^{-1} dextrose application to dormant buds of mangosteen. An addition of dextrose reduced phytotoxicity on leaves and may have increased uptake of thiourea.

In strawberry, shorter photoperiod caused decreases in runner production (Smeet,

1970), flower induction (Durner and Poling, 1987) and initiation of dormancy which prevented any later vegetative growth (Guttridge, 1968; Roberts et al., 1999). In contrast, stolon formation, petiole elongation and leaf area of strawberries was stimulated by increasing daylength and high temperatures (Heide, 1977). Jackson (1989) also reported that long day conditions promoted rapid growth of hops grown at low latitudes. It is also generally accepted that long photoperiods promote shoot growth of potato (Stutte et al., 1996). A similar result was also obtained with 'Fwang Tung' and 'Thai Knight' carambola (Salakpetch et al., 1990).

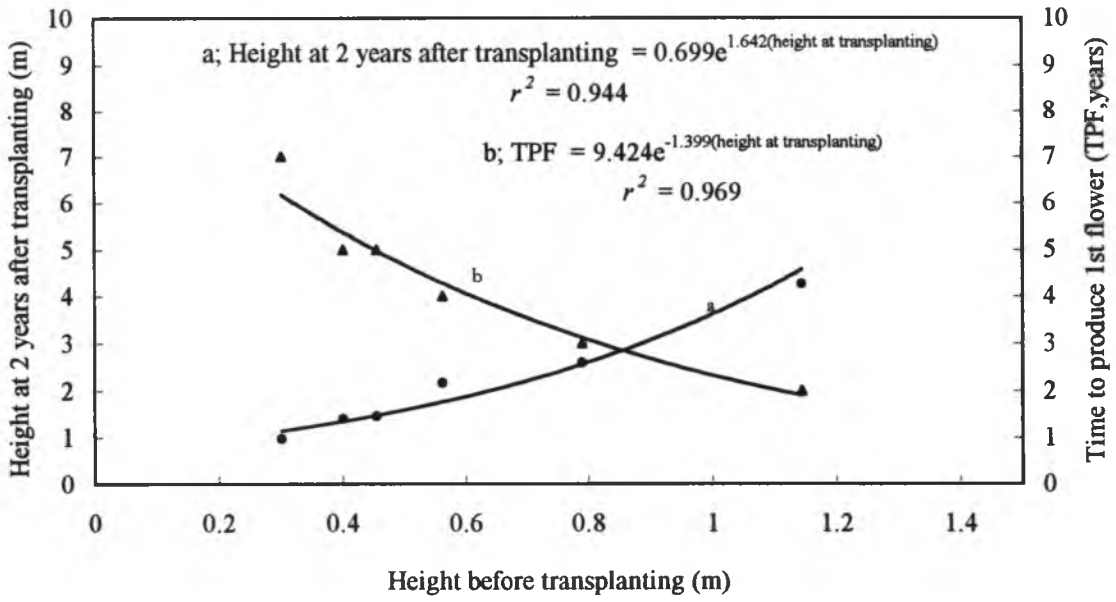

Fig. 5.1 Growth of mangosteen and time to produce the 1st flowering after transplanting as affected by height before transplanting, Chanthaburi, Thailand, 1997.

It was observed that height of mangosteen plants and time to produce the first flowering after transplanting were correlated with height of seedlings at transplanting.

The data can be fitted well by the following exponential function: *height at 2 years after transplanting = 0.699 e* $^{1.642H}$ *which H is height at transplanting and* r^2 *= 0.944*; and the following exponential decay function: *time to produce 1st flowering after transplanting = 9.424 e* $^{-1.399H}$ *which H is height at transplanting and* r^2 *= 0.969* (Fig. 5.1, S. Salakpetch and S. Chandraparnik, unpublished data, 1997). Both relationships suggested that taller seedlings at transplanting produced the first flowering faster than the shorter seedlings. Growth stimulation of seedlings in the nursery may reduce juvenility of mangosteen after field establishment. The objectives of the present study were to 1) evaluate the potential of plant growth regulators and photoperiod to accelerate vegetative growth of juvenile mangosteen; and 2) investigate how growth regulators and photoperiod affected leaf, root, and shoot development.

5.2 Materials and Methods

Plant material. Experiment I&II. Two-year-old seedlings with 11-12 pairs of leaves and 1-2 sets of lateral branches were selected for use in the experiments. Seedlings were grown in 12-L black polyethylene bags (160 mm diameter x 600 mm depth) containing 60, 20, 15, and 5% by volume of coir dust, coarse sand, rice hulls, and rice hull charcoal potting mix, respectively. All plants were placed in a shadehouse covered with 50% black shadecloth which admitted a maximum photosynthetic photon flux density (PPFD) 915.2 μmol m^{-2} s^{-1} at midday. Mean maximum/minimum day/night temperatures were 31.9°/23.1°C. The plants were irrigated with an automatic drip system with an amount of water that was equivalent to about 75% of daily evaporation from a class A

evaporation pan, and fertilized every 3 months with 5 g per container of a granular complete fertilizer and by a monthly foliar spray of 30 g dextrose, 1 ml humic acid, and 2 g foliar complete fertilizer per 1 liter water. The fertilizer consisted of 10N - $20P_2O_5$ - $30K_2O$ - 0.085Mg - 0.950S - 0.078Fe - 0.055Mn - 0.047Cu - 0.095Zn - 0.025B - 0.005Mo. The experiment was conducted at the Chanthaburi Horticultural Research Center (CHRC), Chanthaburi, Thailand in 1995-1997. Six months later, sets of 15 uniform plants which had 3 to 4 sets of lateral branches and whose last pair of leaves had emerged 9 weeks earlier were selected for treatments.

In experiment I, plant growth regulators were hand-sprayed to thoroughly wet the plants, particularly the terminal shoots. The following plant growth regulators were used: gibberellin A_{4+7} (GA_{4+7}) at 500 and 1000 mg l^{-1}, 6-benzyladenine (BA) at 100 and 200 mg l^{-1}, GA_{4+7} + BA at 500 each and 1000 mg l^{-1} each, and 2500 mg l^{-1} thiourea + 30000 mg l^{-1} dextrose. Another set of 15 uniformly plants that were unsprayed served as the control. The stock solutions, 10% of GA_{4+7} and GA_{4+7} + BA, a product containing 18 g l^{-1} GA_{4+7} + 18 g l^{-1} BA, were provided by Thepwathana Chemicals Co., Ltd., Thailand. All plants were sprayed when the latest flush was at least 9 weeks old. The plants were resprayed 5 times during the course of the experiment, which lasted 12 months.

In experiment II, another 4 sets of 15 uniform plants were exposed to 4 different photoperiod regimes daily. Light was supplied by a combination of 12 fluorescent tubes (Philip Super 80 TLD 36 W/86) and 5 incandescent lamps (Philip Day light 40w). The light was turned on automatically at 06:00 pm to extend the daylength for 2, 4, 6, and 8

hours, and automatically turned off after the extended days were complete. Since duration of sunshine at CHRC during the experiment was 12 hours on average, 4 different extended photoperiod regimes were about 14, 16, 18 and 20 hours, respectively. All treated plants were exposed to natural daylight during the day and to artificial light at night, whereas the controls were exposed only to natural daylight. Plants were exposed to the extended photoperiods for a period of 16 months.

Experiment III. Sets of 5 plants from each of the plant growth regulator and photoperiod treatments and the untreated controls were hardened and transplanted to the field at the end of experiment I and II (in May 1998). To simulate the traditional grower practice, two-year-old seedlings which were grown in 8.2 liter black polyethylene bags (203.2 mm diameter x 254 mm depth) containing rice hulls, soil, and cow manure (2:1:1 by volume) and maintained under 50% black shadecloth, were also transplanted to the field (in June 1995). All plants that were transplanted to the field were shaded with 50% black shadecloth for about 1 year after transplanting. A granular $16N\text{-}16P_2O_5\text{-}16K_2O$ fertilizer plus minor and trace elements, and cow manure were applied 3 times a year. Irrigation was applied by a sprinkler system with amount of water equivalent to about 75% of daily evaporation from a class A evaporation pan. The plants were also separated into 2 groups after the completion of the plant growth regulator and photoperiod treatments. One group (3 plants) received careful pest management and the other (2 plants) was grown without careful pest management. The plant growth regulator treatments received careful of pest management for approximately 8 months prior to

transplanting into the field. The photoperiod treatments received careful pest management for approximately 4 months before transplanting into the field. In the traditional grower practice, pest control was started at transplanting.

Measurement :

Experiment I. Time of bud burst and number of flushes were recorded after growth regulator application. Internode length and plant height were measured monthly. Leaf number on each flush was counted and leaf area on the induced flush was estimated when leaves developed to fully maturity using the formula :

$$LA = 0.6994\ (W*L) + 4.674 \ldots (5.1)$$

where, LA = leaf area in cm^2
W = maximum leaf width in cm
L = maximum leaf length in cm
with adjusted r^2 = 0.994** (S. Salakpetch and S. Chandraparnik, unpublished data, 1996)

At the end of the experiment, the 10 plants of each treatment were destructively harvested and divided into stems (main stem, primary and secondary branches), leaves, and roots. Fresh and dry weight were recorded. Specific leaf area (SLA, leaf area per unit dry weight in $cm^2\ g^{-1}$), leaf weight ratio(LWR), stem weight ratio (SWR), and root weight ratio (RWR) (leaf, stem, and root dry weight relative to total plant dry weight) were calculated from the respective growth data.

Experiment II. Flushes of new growth were recorded as they occurred. Internode length and plant height were also measured after each new flush. Leaf number and leaf

dimensions (width and length) on each flush were recorded. Leaf area was then calculated using equation 5.1. At the end of the experiment, the 10 plants of each photoperiod treatment were destructively harvested and divided into stems (main stem, primary and secondary branches), leaves, and roots. Fresh and dry weight were recorded. Specific leaf area (SLA, $cm^2\ g^{-1}$), leaf weight ratio (LWR), stem weight ratio (SWR), root weight ratio (RWR), and leaf area ratio (LAR, $m^2\ kg^{-1}$, total leaf area relative to total plant dry weight) were calculated from the respective growth data. The LWR, SWR, and RWR are measures of leaf, stem, and root of the plant on a weight basis.

Experiment III. Plant height and diameter were measured monthly after transplanting into the field. The canopy area, based on the surface area of the cylinder, was then calculated.

Statistical analysis :

Experiment I. Data were subjected to analysis of variance procedures and treatment means were separated using the least significant difference test ($P \leq 0.05$).

Experiment II. Data were subjected to regression analysis to determine the appropriate photoperiod to maximize growth of young mangosteen.

Experiment III. Means of canopy area of all trees with and without careful pest control groups were compared.

5.3 Results

Experiment I. *Days to leaf emergence.* Plant growth regulators did not

significantly affect days to leaf emergence, which is days when leaf buds started emergence after the application of plant growth regulators, in the treated plants. The duration between treatment and leaf emergence ranged from 10.2 to 12 days after treatment with the plant growth regulators (Table 5.1)

Leaf number, leaf area and growth. GA_{4+7} and the highest dose of GA_{4+7} + BA were significantly effective in increasing the number of flushes in mangosteen plants (4.3 to 5.2 flushes) compared to 3.0 flushes in the control. Leaf number on each induced flush was increased in response to GA_{4+7} alone, but the effect was greater in combination with BA or with BA alone or with thiourea + dextrose (Table 5.1). All treated trees produced significantly more flushes and more leaves on each flush than did control plants. Consequently there were a significantly greater number of total leaves produced by the end of the treatments compared to the untreated controls. However, area of individual leaves was smaller in mangosteen plants receiving both GA_{4+7} or BA alone or a combination of GA_{4+7} and BA compared to leaves from the thiourea and the control treatments. Total leaf area of all treated trees, however, was significantly increased due to the larger total leaf production. Internode length was shortest in the GA_{4+7} + BA treatment and with 1000 mg l^{-1} GA_{4+7} compared to the other plant growth regulator treatments and the control. At the end of 12 months, height of all plant growth regulator treated trees was significantly increased compared to the controls except for the 500 mg l^{-1} of GA_{4+7} + BA (Table 5.1).

Table 5.1 Days to leaf emergence, leaf area, internode length, number of flushes, number of leaves on each flush, and total leaf number on 2-year-old mangosteen 12 months after treatment with plant growth regulators (means of 10 plants).

Growth regulator (mg l^{-1})	Days to leaf emergence	Number of flushes	Leaf number on each flush	Total leaves produced	Mean leaf size on induced flush (cm^2)	Total leaf area (m^2)	Internode length of induced flush (cm)	Tree height (m)
GA_{4+7}								
500	11.3	4.3	9.0	38.5	90.7	0.36	12.2	1.15
1000	10.2	5.2	9.6	49.8	64.6	0.33	8.9	1.23
BA								
100	11.3	3.6	12.9	46.3	99.2	0.45	12.1	1.15
200	12.0	3.8	13.7	52.2	82.4	0.46	11.5	1.15
GA_{4+7} + BA								
500	10.2	3.7	13.9	51.6	57.6	0.34	8.1	1.01
1000	10.4	4.6	19.1	88.1	59.6	0.52	8.1	1.13
Thiourea 2500 + dextrose 30000	11.0	3.5	13.0	45.5	104.9	0.48	11.3	1.14
Untreated	-	3.0	7.5	22.6	101.3	0.23	11.3	0.99
LSD at $P \leq 0.05$	NS	0.33	1.24	3.93	6.65	0.004	0.43	0.08

Total dry matter and its partition. The 10 plants were destructively harvested at the end of the experiment to determine dry matter partitioning after treatment with plant growth regulators. Total dry weight of all treated plants was larger than the controls since they produced more flushes and leaves, and were taller (Table 5.2). Stem, root and leaf dry weights of plants in all plant growth regulator treatments were significantly greater than the controls. However, all plant growth regulator treatments did not result in significantly changes in the partitioning of the stem, root, and leaf dry matter (Table 5.2).

Table 5.2 Total plant dry weight, dry weight partitioning and specific leaf area (SLA) of 2-year-old mangosteen plants at 12 months after treatment with plant growth regulators (means of 10 plants).

Growth regulator ($mg\ l^{-1}$)	Total plant dry weight (g)	Dry weight (DW) partitioning						SLA ($cm^2\ g^{-1}$)
		Stem DW (g)	*Stem weight ratio (SWR)*	Root DW (g)	*Root weight ratio (RWR)*	Leaf DW (g)	*Leaf weight ratio (LWR)*	
GA_{4+7}								
500	375.1	141.2	*0.38*	125.2	*0.33*	108.6	*0.29*	61.1
1000	419.6	180.3	*0.43*	119.7	*0.28*	119.6	*0.28*	57.8
BA								
100	463.3	165.8	*0.36*	165.0	*0.36*	132.6	*0.28*	53.6
200	427.5	178.7	*0.42*	118.3	*0.28*	130.5	*0.30*	57.1
GA_{4+7} + BA								
500	352.7	153.7	*0.44*	96.0	*0.27*	103.0	*0.29*	69.1
1000	395.4	175.6	*0.44*	110.4	*0.28*	109.4	*0.28*	79.7
Thiourea 2500 + Dextrose 30000	450.9	187.1	*0.41*	137.9	*0.31*	126.0	*0.28*	61.4
mean $\pm$ SE			*0.41 $\pm$ 0.01*		*0.30 $\pm$ 0.01*		*0.29 $\pm$ 0.003*	
Untreated	260.8	113.7	*0.44*	80.4	*0.31*	66.7	*0.25*	92.4
LSD at $P \leq 0.05$	26.90	7.91	NS	7.51	NS	5.88	NS	4.02

Experiment II. *Growth of mangosteen.* Height of mangosteen trees was promoted when exposed to 2- and 4-hour-photoperiod regimes. Internode length and flush number tended to decrease when the photoperiod extensions were longer than 2 and 4 hours, respectively (Table 5.3). Increases in leaf number on each induced flush and total leaf number at the end of the experiment were markedly larger in all treated trees. The largest increase was observed in the 4-hour-photoperiod extension treated trees. No significant differences were observed in the area of individual leaves. Total area of all leaves

produced under the photoperiod regimes and the subsequent total leaf area of the whole tree were the largest on the trees exposed to 2-hour-photoperiod treatment while those on the 8-hour-photoperiod trees were the least but larger than the control (Table 5.3).

Table 5.3 Effects of extended photoperiod regimes on growth of 2-year-old mangosteen plants over a 16-month-period (means of 10 plants).

Photoperiod extension regimes (hours)	Height (m)	Internode length of induced flush (cm)	Number of flushes	Leaf number on each flush	Total leaves produced	Mean leaf size on induced flush (cm^2)	Leaf area production (m^2)	Total leaf area (m^2)
2	1.12	14.5	3.9	18.1	70.7	114.3	0.81	1.09
4	1.19	14.3	4.3	19.7	85.2	93.1	0.79	1.08
6	1.06	13.2	3.5	16.9	59.3	101.8	0.60	0.92
8	1.03	11.8	3.2	15.3	48.0	91.5	0.45	0.66
Untreated	0.99	11.3	3.0	7.6	23.5	101.3	0.29	0.53

Table 5.4 r^2 and photoperiod extension for maximum growth response, derived by quadratic relationship, defining the relationship between percent change in growth of 2-year-old mangosteen plants over the control and photoperiod regimes (means of 10 plants at each photoperiod regime).

Growth characteristics	r^2	Photoperiod extension for maximum response (hours)
Height (m)	0.815	4
Leaf number on each flush	0.841	4
Total leaves produced	0.802	4
Leaf area produced (m^2)	0.975	2
Total leaf area (m^2)	0.999	2

Regression relationships between the change in growth (%) of mangosteen plants over the control and photoperiod regimes (hours) were developed to determine an

appropriate photoperiod to maximize the growth characteristics of mangosteen plants (Table 5.4). The relationship showed that 4-hour-photoperiod promoted maximum height, leaf number on each flush and the total leaves produced (Table 5.4). A 2-hour-photoperiod regime, however, promoted maximum total area of all leaves produced and leaf area of the whole tree.

Plant dry weight and its partition. Total plant dry weight was increased by 7 to 72% over the control as a consequence of exposure to different photoperiod regimes (Table 5.5). The stimulatory effects of different photoperiod treatments were greatest on leaf dry weight, followed by stem and root dry weights. Greater effect was observed on the 2-hour-photoperiod treated trees compared to 8-hour-photoperiod treated trees (Table 5.5). Photoperiod treatments also resulted in changes in the partitioning of dry matter (Table 5.6). Stem, leaf, and root dry weight accounted for an average of 0.40 SWR, 0.37 LWR, and 0.23 RWR, respectively, compared to 0.45 SWR, 0.24 LWR, and 0.31 RWR, respectively, for the control. Among the 4 different photoperiods, the SWR was decreased in trees exposed to daylength extension longer or shorter than 4 hours. The LWR tended to increase, whereas RWR tended to decrease when daylength was extended (Table 5.6). The root : shoot ratio was not increased in all treated trees when compared to the control. Trees exposed to 2-hour-photoperiod had greater root : shoot ratio (0.38) than other treated trees. When photoperiod extension was increased from 2 to 8 hours, specific leaf area (SLA) decreased dramatically while leaf area ratio (LAR) exhibited no significant changes (Table 5.7).

Table 5.5 Effects of extended photoperiod on total dry matter production of 2-year-old mangosteen plants 16 months after initiation of photoperiod treatments (means of 10 plants).

Photoperiod extension regimes (hours)	Total dry weight (g)	Total dry weight change over the control (%)	Stimulatory effect of photoperiod					
			Stem DW (g)	Stem DW change over the control (%)	Leaf DW (g)	Leaf DW change over the control (%)	Root DW (g)	Root DW change over the control (%)
2	444.8	72.1	179.8	54.6	143.8	132.9	121.2	50.7
4	376.8	45.8	163.1	40.2	138.1	123.6	75.6	-6.0
6	359.7	39.2	143.5	23.4	128.1	107.4	88.1	9.6
8	276.6	7.0	102.1	-12.2	118.6	92.2	55.8	-30.6
Untreated	258.5	-	116.3	-	61.7	-	80.4	-

Table 5.6 Dry matter partitioning and root : shoot ratio of 2-year-old mangosteen plants 16 months after initiation of photoperiod treatments (means of 10 plants).

Photoperiod extension regimes (hours)	Root : shoot ratio	Dry weight (DW) partitioning					
		Stem DW (g)	*Stem weight ratio (SWR)*	Leaf DW (g)	*Leaf weight ratio (LWR)*	Root DW (g)	*Root weight ratio (RWR)*
2	0.38	179.8	*0.40*	143.8	*0.32*	121.2	*0.27*
4	0.25	163.1	*0.43*	138.1	*0.37*	75.6	*0.20*
6	0.33	143.5	*0.39*	128.1	*0.36*	88.1	*0.25*
8	0.25	102.1	*0.37*	118.6	*0.43*	55.8	*0.20*
mean $\pm$ SE			*0.40 $\pm$ 0.01*		*0.37 $\pm$ 0.02*		*0.23 $\pm$ 0.02*
Untreated	0.45	116.3	*0.45*	61.7	*0.24*	80.4	*0.31*

Table 5.7 Specific leaf area (SLA) and leaf area ratio (LAR) of 2-year-old mangosteen, 16 months after initiation of photoperiod treatments (means of 10 plants).

Photoperiod regimes (hours)	SLA ($cm^2\ g^{-1}$)	LAR ($m^2\ kg^{-1}$)
2	81.33	2.50
4	77.42	2.85
6	73.53	2.61
8	56.17	2.39
Untreated	92.38	2.12

Experiment III. The mangosteen trees grown under traditional grower practices were transplanted into the field in 1995 when they were 2 years old. One year after transplanting, their canopy area was 3.9 and 3 m^2 for trees with and without pest management, respectively, compared to the larger sized 3-year-old trees from the plant growth regulator and photoperiod treatments and the untreated controls, at transplanting (Table 5.8 and 5.9). At 1 year after transplanting when all treated trees were 4 years old, canopy areas increased dramatically from about 5 m^2 to about 23 m^2 in the growth regulator and photoperiod treated trees and from about 4.4 m^2 to about 20.9 m^2 in the untreated control trees that received good pest management. Mean canopy area of treated trees without pest management was 3.6 m^2 when they were 3 years old and increased to 14.9 m^2 one year later. The canopy area of 3- and 4-years-old untreated control trees without pest management was about 3.3 and 13.5 m^2, respectively. In contrast, canopy size of the traditional grower practice trees after 4 years was 15.6 and 7.1 m^2 when grown

with and without pest control, respectively (Table 5.8 and 5.9). This indicates that the field grown trees that were previously treated with growth regulators or with extended photoperiods were able to increase their size very rapidly after transplanting. This potential may lead to increased production of leaves and branches and attainment of greater tree size (canopy area) earlier than in untreated trees.

Table 5.8 Means of canopy area (m^2), based on surface area of the cylinder, of plant growth regulator treated mangosteen trees at different ages after seeding, with (+, means of 3 trees) and without (-, means of 2 trees) pest control after field establishment.

Growth regulators (mg l^{-1})	Canopy size at different ages			
	3(+)	3(-)	4(+)	4(-)
GA4+7				
500	5.08	3.63	23.19	15.08
1000	5.05	3.73	23.11	15.39
BA				
100	5.07	3.61	23.18	15.01
200	5.08	3.62	23.23	14.35
GA_{4+7} + BA				
500	4.80	3.41	22.15	14.88
1000	5.03	3.59	23.01	14.96
Thiourea 2500 + dextrose 30,000	5.23	3.61	23.80	15.00
mean ± SE	5.05 ± 0.05	3.60 ± 0.04	23.09 ± 0.18	14.95 ± 0.12
Untreated ± SE	4.44 ± 0.05	3.26 ± 0.05	20.89 ± 0.26	13.46 ± 0.18
Traditional grower practice ± SE	3.95 ± 0.05	2.97 ± 0.04	15.62 ± 0.29	7.11 ± 0.12

Table 5.9 Means of canopy area (m^2), based on surface area of the cylinder, of photoperiod treated mangosteen trees at different ages after seeding, with (+, means of 3 trees) and without (-, means of 2 trees) pest control after field establishment.

Photoperiod regimes (hours)	Canopy size at different ages			
	3(+)	3(-)	4(+)	4(-)
2	5.17	3.61	23.59	15.2
4	5.03	3.70	23.05	14.60
6	4.90	3.48	22.51	15.31
8	4.85	3.47	22.31	14.51
mean ± SE	4.99 ± 0.07	3.56 ± 0.05	22.86 ± 0.29	14.90 ± 0.20
Untreated ± SE	4.44 ± 0.05	3.26 ± 0.05	20.89 ± 0.26	13.46 ± 0.18
Traditional grower practice ± SE	3.95 ± 0.05	2.97 ± 0.04	15.62 ± 0.29	7.11 ± 0.12

5.4 Discussion

Wiebel et al. (1992) showed that a combination of GA_{4+7} and BA induced bud-break of 1 to 3-year-old mangosteen within a week, whereas GA_{4+7} and BA alone were less effective. In the present study bud-break was observed more than 7 days after treatment. This may have been due to different application techniques. To facilitate application of plant growth regulators in the Wiebel et al. (1992) study, leaf petioles were pulled apart to partially expose the bud. The chemicals were then applied by inserting a pipette between the leaf bases. To ensure that the droplet with chemicals coated the buds, the petioles were pulled apart several times following release of the chemicals. In the present study growth regulators were applied to drip with a hand sprayer and might not

have come into direct contact with the apical bud which is embedded at the bases of the terminal pair of leaves. Although the growth regulators were not applied directly to the apical bud, flushing was still increased after foliar application.

Applications of all plant growth regulators stimulated vegetative flushing and increased the number of leaves on each flush. This resulted in greater leaf production when compared to the controls. GA_{4+7} or BA alone or in combination significantly overcame bud dormancy in mangosteen but did not increase leaf size. Wiebel et al. (1992) also found that area of individual leaves of 8-month-old mangosteen seedlings was reduced after GA_{4+7}, BA, or GA_{4+7} + BA application. The reduction in leaf size may have been due to the decreased availability of nutrients including carbohydrates, which could be limiting if higher numbers of flushes and leaves on each flush were produced. Bird and Hardwick (1982) suggested that flush size was, in part, determined by carbohydrate availability in cacao. Application of thiourea in combination with dextrose was made to reduce thiourea damage to leaves and increase the uptake rate of thiourea. Dextrose may have also served as a carbohydrate source and promoted normal growth of leaves on each induced flush.

Previous work showed that internode elongation was not affected by GA_3, GA_{4+7}, BA, and GA_{4+7} + BA, except for GA_3 at higher doses (Wiebel et al., 1992). A similar result was also observed in this study. Sachs (1965) showed that an aspect of gibberellin action was to increase stem elongation by increasing subapical meristem activity. Sensitivity to gibberellins is also dependent upon plant species and stage of development

as well as concentration (Lin et al., 1984). The concentrations of GA used in the present study did not promote internode elongation of mangosteen. Although the length of internode was not increased with plant growth regulator applications, height of all treated trees significantly increased compared to the controls. This suggests that increased flush numbers, rather than internode length, contributed to increased height of mangosteen.

A new flush of juvenile mangosteen plants on the primary axis is normally comprised of 1 vertical and 2 lateral shoots, each bearing 2 developing leaves. The emergence of secondary branches on the lateral branches does not always accompany the new flush. They may develop when plants are healthy or grown under stimulatory growth conditions e.g., CO_2-enrichment (Downton et al. 1990; P. Polprasid, personal communication, 2000). The results in the present study showed that GA_{4+7} or BA alone or in combination could promote flushing in mangosteen (Table 5.1). Leaf number produced on each flush was markedly increased after BA or GA_{4+7} + BA application compared to the untreated controls. BA or GA_{4+7} + BA enhanced not only number of flushes but also the number of secondary branches of the new flush, which resulted in a greater number of leaves on each flush. The present study is in agreement with previous reports in apple by Kender and Carpenter (1972) and Cody et al. (1985) who succeeded in producing lateral branches after BA or GA_{4+7} + BA application. Kinet et al. (1993) proposed that since the root system was the principle site of cytokinin synthesis, any treatment that promoted root growth and resulted in cytokinin production would be expected to reduce or inhibit the response to GA_{4+7}. High concentrations of BA, 500 and

1000 mg l^{-1}, added to a combination with GA_{4+7} may reduce its influence, resulting in shorter internode of mangosteen plants when compared to the application of GA_{4+7} or BA alone. Gibberellins had no effect on breaking rest of apple and peach flower buds (Hatch and Walker, 1969; Shaltout and Unrath, 1983; Walker, 1970) but stimulated the expansion of buds of apple and blackcurrant (Wainwright and Price, 1984; Williams and Billingsley, 1970). Gibberellins were also used to break dormancy in potato and rhubarb, which received an inadequate chilling period (Rappaport et al., 1957; Tompkins, 1966) and to stimulate bud break in *Salix pentandra* and *Rhus typhina* (Junttila, 1981; Nitsch, 1957). A similar result was also obtained in the present study when GA_{4+7} was applied to young mangosteen plants (Table 5.1).

Hendrick and Taylorson (1974, 1975) and Nir et al. (1986) reported that thiourea decreased catalase activity which caused an increase in the level of H_2O_2 in bud tissues. They further hypothesized that the increased level of H_2O_2 activated the pentose phosphate pathway, which was associated with termination of bud dormancy and rapid growth (Simmonds and Simpson, 1972). Thiourea application in nectarine resulted in an inhibition of catalase activity and a stimulation of glucose-6-phosphate dehydrogenase activity but no effect on 6-phosphogluconate dehydrogenase (two key enzymes in the pentose phosphate pathway) (Hu and Couvillon, 1990). However, there was no correlation between the enzymic activity and dormancy breaking of nectarine seeds and buds. The rapid metabolism of thiourea in the plants and bud tissue sensitivity may possibly contribute to the effectiveness of thiourea on bud break (Erez, 1975; de Villiers

and Meynhardt, 1965). Erez (1975) described that thiourea could break dormancy of vegetative buds and enhance growth and development of the buds when applied at the right timing (buds were competent), and suggested that this is an advantageous characteristic over other bud-breaking chemicals. Similar results were also obtained in peach and apple (Fernandez-Escobar and Martin, 1987; Shaltout and Unrath, 1983). The present study also showed that thiourea + dextrose application could promote vegetative flushing and more extensive lateral branch development resulting in a greater number of leaves on each flush and total leaves produced than the controls.

Growth, number of flushes, total leaf production, and total leaf area were generally increased after applications of plant growth regulators, consequently total dry weight of the whole tree was larger than the control. Also, the leaf area per unit weight (SLA) was significantly decreased in the treated trees. Thick leaves are reported to have larger surface areas of mesophyll cells exposed to intercellular air spaces and provide better opportunities for CO_2 exchange at photosynthetic sites (Treharne, 1982). Increased dry weight of treated plants may have been due to an overall higher rate of photosynthesis per unit leaf area. Stem weight ratio (SWR) and leaf weight ratio (LWR) were not significantly different from the control. Regulation of assimilate production and movement from source to sink tissues has been reported as a result of plant growth substance application, i.e. gibberellin, cytokinin, auxin, or abscisic acid (Huang et al., 1988; Thomas, 1985). However, plant growth regulator treatments did not have any particular effect on alteration of assimilate partitioning into the various organs of

mangosteen trees. The LWR increased slightly but was not significantly different.

Because of its extremely slow rate of development with a long period of time elapsing between production of a new pair of leaves, mangosteen seedlings are often approximately only 15 cm tall after 2 years (Almeyda and Martin, 1976). Darnell (1991), Fennell and Hoover (1991), and Fuchigami et al. (1986) demonstrated that growth cessation and terminal bud set were frequently observed in trees and woody shrubs under short photoperiod treatment of 12 or 13 hours. In woody species, particularly in the temperate zone, rate and duration of stem elongation usually increases with increasing daylength. Plants of some species continue to grow more or less indefinitely when maintained under LD, while in some, the onset of dormancy is delayed but not entirely prevented. Furthermore, extension growth proceeds in a series of flushes, and the duration of the dormant period between successive flushes is shortened by LD e.g., *Pinus sylvestris, Citrus limon, C. paradisi*, and *Camellia japonica*.

Since the day length varies much less in tropical regions than the temperate zones, it is often dismissed as being of little importance. However, Longman (1969, 1978) showed that in some tropical species e.g., *Ceiba pentandra, Gmelina arborea*, and *Bombax buonopozense* growth cessation was favored by exposure to SD and cool nights, whereas internode length was influenced by LD. When plants are grown under extended daylengths, development is modified by light quality and in particular by changes in the relative amounts of light energy in the red and far-red parts of the spectrum which is brought about by leaf shading or reflectance of the incident light (Smith, 1992). These

changes may cause increases in stem extension, enhanced apical dominance, and changes in patterns of assimilate partitioning (Thomas and Vince-Prue, 1997). Tungsten filament lamps (an incandescent lamp) normally establish a much lower Pfr/Ptotal ratio than fluorescent light. Therefore, extended daylengths with tungsten lamps can result in longer internodes and taller plants than with fluorescent lights since the tungsten lamps establish a lower Pfr/Ptotal ratio in addition to their effect on photoperiod. In the present study, the extended light was a combination of incandescent and fluorescent light. Internode length of mangosteen grown under the extended day was slightly enhanced when compared to the control. In addition, number of flushes decreased when mangosteen trees received photoperiod longer than 4 hours, but flush nunber was slightly greater than those on the controls (approximately 12-hour-photoperiod). This suggests that mangosteen plants may require greater light durations to stimulate growth but very long extended day lengths can slow vegetative growth. Height of mangosteen trees exposed to the 4-hour-photoperiod extension treatment was greatest even though their internode elongation and the largest number of flushes were not significantly different from the control (Table 5.3). As with plant growth regulators, this result suggests that internode length and flush number in combination appear to contribute to height of mangosteen in the nursery stage.

Enlargement of individual leaves with increasing daylength has been reported in several plants species. One effect of LD is to increase leaf surface expansion and increase development of thinner leaves which result in increased SLA (Heide et al., 1985). The higher SLA in long days is principally the consequence of increased cell size although

there may be a modest contribution from decreased thickness and number of cell layers (Hay and Heide, 1983). When alterations in the daylength bring about large developmental changes, modification to the distribution of resources within the plant is a consequence. Thus, the assimilate partitioning may be a consequence of the developmental change rather than a direct response to daylength (Thomas and Vince-Prue, 1997). A rapid change e.g., within 24 hours of a change in daylength, in the partitioning of assimilates between different organs, however, would indicate a direct effect of photoperiod on the process of assimilate partitioning (Britz et al., 1985). When studying long-term changes in partitioning, Hay and Heide (1983) found that the stimulation of dry weight, plant height and leaf area by LD in *Poa pratensis* occurred without any change in the partitioning of assimilates amongst leaves, stems and stolons. It appeared that the increase in leaf dry weight was a consequence of overall increases in plant dry weight rather than the reallocation of the dry weight in leaf tissue.

Dale (1965) demonstrated that both leaf area ratio (LAR) and SLA decreased, whereas LWR of *Phaseolus vulgaris* L. remained unchanged when photoperiod was increased. Leaf area and total plant dry weight were also significantly greater when compared to the plants developed in shorter photoperiod. Frankland and Letendre (1978) also obtained higher SLA from the woodland species, *Circaea lutetiana*, grown in shorter daylength. Dale (1988) has suggested that plant species differ in how dry weight is distributed between leaves and other tissues in response to shade as well as photoperiod treatment. In the present study, when daylength was increased by 2 to 8 hours, areas of

individual leaves tended to decrease while total leaf area significantly decreased. With the 2-hour-photoperiod extension, SLA was higher, but LWR was less than with other photoperiod treatments. This resulted in the development of larger leaf area (114.31 cm^2) but thinner leaves compared to the other treatments. Also, greater dry weight distribution to roots occurred which resulted in higher root weight ratio (RWR) compared to other photoperiod extension treatments. As photoperiod was increased beyond the 2 hour treatment, SLA decreased while LWR tended to increase dramatically, indicating that more assimilates were transferred into the leaves. The decline in leaf area also suggested that leaves increased in thickness. The results also showed that total plant dry matter decreased when the days were extended beyond 2 hours. With 2 hour photoperiod treatment, maximum dry weight accumulation and growth occurred in mangosteen seedlings. This was attributed to an increase in the total number of leaves produced and to an increase in total leaf area.

According to Downton et al. (1990) the relatively low carbon acquisition capacity of leaves, low LAR (2.12 $m^2\ kg^{-1}$), and the prolonged bud dormancy at the shoot apex, even under constant favorable growing conditions, probably contribute to the slow growth rate of mangosteen trees. Maximization of photosynthetically active area per total plant dry matter i.e., LAR, can be achieved by increasing the proportion of total dry matter allocated to leaves (LWR) or by reducing leaf thickness, or both (Bjorkman, 1981; Hay and Heide, 1983). The LAR in the present study did not increase with extending photoperiod although LWR increased. SLA decreased dramatically which indicated that

leaf thickness increased. The LAR (2.39 – 2.85 m^2 kg^{-1}) obtained in the present study was extremely low when compared to fast-growing species (Poorter and Remkes, 1990) and to Wiebel et al. 's (1994) study where they obtained LAR of 2.9 – 4.0 m^2 kg^{-1}.

Root growth (RWR = 0.20) of mangosteen was enhanced as a consequence of CO_2 enrichment and a root : shoot ratio of 0.25 was obtained (Downton et al., 1990). Mangosteen seedlings grown under 50% shade exhibited a very low RWR of 0.15 and only a 0.18 root : shoot ratio (Wiebel et al., 1994). A low RWR is potentially deleterious under inadequate nutrient and water supply conditions (Bjorkman, 1981) and may lead to slow growth and development. Such conditions are likely to occur when mangosteen seedlings are shifted from the well protected nursery environment to the field. The relatively small proportion of dry matter allocated to roots in mangosteen plants developed under the photoperiod treatments resulted in low RWR of 0.20 - 0.27 and a root : shoot ratio of 0.25 - 0.38 when compared to the untreated control which had RWR and root : shoot ratio of 0.32 and 0.45, respectively. Although root growth of the photoperiod treated plants were suppressed when compared to the untreated controls, root development was better than that observed with CO_2 enrichment (Downton et al., 1990). The difference may be due to the composition of the potting mix which permitted better growth and development of roots. The composition of the potting mix in the present study was 6 : 2 : 1.5 : 0.5 by volume of coir dust, coarse sand, rice hulls, and rice hull charcoal, respectively. In the study by Downton et al. (1990) the mix consisted of 1 part peatmoss : 1 part coarse sand : 1 part of peanut husks, and in the investigation by

Wiebel et al. (1994) the potting media consisted of a 1 : 1 : 1 by volume of peat moss, coarse sand, and pine bark, respectively.

This study indicated that a mixture of coir dust, coarse sand, rice hulls, and rice hull charcoal at the ratio of 6 : 2 : 1.5 : 0.5 by volume, respectively, could be recommended as a potting mix. The 160 mm diameter x 600 mm depth black polyethylene bags should also be used to allow the taproot to grow downward and uninterrupted. Plant growth regulators or extended daylength should be applied to accelerate growth of mangosteen seedlings. Although all plant growth regulator treatments could increase the number of vegetative flushes, leaf number on each flush, total leaves produced and total leaf area, the advantage of thiourea + dextrose over other growth regulators was that it did not reduce the leaf size of the induced flush. Based on its advantage, thiourea + dextrose is the best recommendation to accelerate growth of young mangosteen plants under the nursery conditions. Mangosteen plants exposed to a 2-hour-photoperiod extension treatment had larger leaves and subsequent total leaf area, higher SLA and RWR, and higher root : shoot ratio when compared to other photoperiod regimes and the controls. The 2-hour-photoperiod extension treatment can be recommended as a favorable condition to stimulate continuous growth of young mangosteen. After plant growth regulator and/or photoperiod treatments, the seedlings would then possess an improved root: shoot ratio greater than 0.22 and have several sets of secondary branches and more leaves, thus increasing LWR and achieving higher LAR. Under these conditions, mangosteen would possess better canopy structure and should

exhibit better growth in field conditions after transplanting. After transplanting, mangosteen should be well protected from major pests, *Scirtothrips* sp. (thrips), *Phyllocnistis* sp. and *Melanocercops* sp. (leaf miner), and *Stictoptera columba* (leaf eating caterpillar), and grown under 50% shade conditions about a year. Water and fertilizer should be applied regularly. Mangosteen trees under such conditions should grow rapidly and have the potential to attain the minimum canopy area (about 50 m^2) associated with earlier maturation.

CHAPTER 6

AGRO-MANAGEMENT PRACTICES TO PROMOTE FLOWERING OF MANGOSTEEN

6.1 Introduction

According to Hackett (1985) juvenility is that period when plants are unable to perform reproductive activity when exposed to favorable inductive conditions. Attainment and maintenance of the ability or potential to flower is the only criterion available to assess the juvenile-to-mature transition. Once maturity is attained, response to favorable inductive conditions will result in consistent flowering, which in turn is necessary for regular production.

Soil moisture stress has been implicated as a factor that induces flowering in several fruit trees. Water stress promotes flowering in lychee by inhibiting vegetative flushing (Menzel et al., 1989; Nakata and Suehisa, 1969). Proebsting et al. (1977) also showed that water deficit conditions induce flowering in 3-year-old apple seedlings. It has been demonstrated that soil moisture stress is a prerequisite for flowering in cashew (Nambiar, 1977) and mango (Singh, 1977). Alvim (1977) also reported that flower initiation in cacao was enhanced by a dry period while flower growth and development were inhibited if the soil moisture was in deficit. Similarly, a period of water stress is also necessary for flower bud development in coffee (Alvim, 1977; Maestri and Barros, 1977; Schuch et al., 1992). Water stress (-3.5 MPa midday leaf WP) for about 4 to 5 weeks can promote flowering and increase flower number per tree on containerized

'Tahiti' lime (Southwick and Davenport, 1986, 1987). Chandraparnik et al. (1992) reported that a continuous dry period, to achieve a mild stress condition, was crucial for flower initiation in durian, whereas irrigation was required to promote growth and development of the flower buds to anthesis. However, rainfall more than 10 mm/day for about 3 to 5 continuous days suppressed development of flower buds at the first stage of emergence. It has been shown that carambola and rambutan (Salakpetch et al,. 1990, 1992) as well as mangosteen (Poonnachit et al., 1996) also required a period of water stress before flowering.

The objective of this study was to develop a practical method to promote flowering in mangosteen by means of water stress. This practical method can be used in an agro-management system to manipulate flowering of mangosteen trees after achieving the minimum size and to manage flowering in a commercial setting.

5.2 Material and Methods

Plant material. The study was conducted in a plot with 23-year-old mangosteen trees, at the Chanthaburi Horticultural Research Center, Chanthaburi, Thailand (≅ 12°N and 101°E), in the 1997/1998-production year. All trees were fertilized with a 16N-16P_2O_5-16K_2O granular complete fertilizer plus minor and trace elements + cow manure, 8N-24P_2O_5-24K_2O, and 13N-13P_2O_5-21K_2O immediately after harvest, 2 months later, and during fruit growth and development, respectively. All selected trees were pruned immediately after the first fertilizer was applied. Irrigation was applied by a sprinkler

system, and the schedule was based on water requirement at different stages of development. The requirements at vegetative growth, flower development, and at fruit growth and development were 60%, 75%, and 80% of the daily evaporation from a class A evaporation pan, respectively. The surface area under each tree was 44 m^2 on average, and approximately 75% of that area were covered by the sprinkler system. Before the experiment commenced, trees were irrigated with 60% of the daily evaporation only when the rainfall ceased for longer than 7 consecutive days. All experimental trees were foliarly sprayed with a combination of 2500 mg l^{-1} thiourea and 30000 mg l^{-1} dextrose and irrigation, when the terminal shoots were at least 9 weeks after emergence, to induce synchronized leaf flushing (Poonnachit et al., 1992; S. Salakpetch, unpublished data).

Experimental design. The experiment was conducted using a randomized complete block design, with seven single-tree replicates. Water was withheld from 14 November 1997, the beginning of the dry season, until the desired wilting response was exhibited. About 2 weeks after the stress condition commenced, there was 10 mm of rainfall on 29 November 1997. The desirable wilting tree responses were;

Response I: the last internode of the terminal shoot beginning to wilt

Response II: the last internode noticeably wilted and the last pair of leaves bent slightly downward

Response III: the last internode and the last pair of leaves exhibited more severe wilting symptoms than in response II, and the shrinkage of the last internode was clearly observable.

When the desired tree response was attained, two different water management regimes were applied. In ***the first regime***, irrigation was applied every third day until flowering. The irrigation rate was 1.85 times the total daily evaporation that occurred during the two intervening days. For example, if the daily evaporation for day 1 was 2 mm and 3 mm for day 2, the evaporation for the two intervening days was 5 mm. The amount of irrigation applied on the 3rd day was 1.85 x 5 mm/tree. ***The second irrigation regime*** consisted of a single application of 35 to 40 mm/tree followed by half of that amount (17.5-20 mm) applied at 7-day-intervals until flowering. The unstressed trees were first irrigated on November 21 and were irrigated throughout the experiment.

The experiment consisted of the following treatments.

Treatment 1: response I trees + 1.85 times the daily evaporation irrigation applied every 3rd day until flowering

Treatment 2: response I trees + 35 to 40 mm/tree and half of the first irrigation applied at 7-day-intervals until flowering

Treatment 3: response II trees + 1.85times the daily evaporation irrigation applied every 3rd day

Treatment 4: response II trees + 35 to 40 mm/tree and half of the first irrigation applied at 7-day-intervals

Treatment 5: response III trees + 35 to 40 mm/tree and half of the first irrigation applied at 7-day-intervals

Treatment 6: control consisted of unstressed trees, which were irrigated twice a

week with 1.85 times the total daily evaporation.

Measurements. Plant vigor was visually evaluated mainly based on leaf vigor (color and size) and damage due to the major pests. Canopy structure, healthy or damage branches, were included in the evaluation (Appendix C). Age of the apical buds after the last pair of leaves started emergence when water was withheld, and at the attainment of the desired stress was recorded. The stress period was then calculated from the respective data. Leaf water potential was determined on four leaves from each tree at midday using the pressure chamber technique (Scholander et al., 1965) when the desired tree response was attained and after irrigation to alleviate water stress. Total water volume applied prior to flowering, flowering date (date of appearance of flower buds), and days to full bloom of the entire tree were also recorded. Days when the first flower bud appeared were recorded from the last rainfall, which was the starting point of stress condition. Duration (days) between the onset of irrigation and appearance of the first flower bud was also recorded. Percentage of leaf drop after water withdrawal and irrigation was observed. Fruit number per tree was also recorded. Analysis of variance, *F* test and least significant differences (LSD) calculated at P = 0.05, was used for statistical analysis.

6.3 Results

Tree performance and leaf xylem water potential. The vigor of mangosteen was 3.6 to 3.7 before the experiment was started (Table 6.1). Emergence of apical buds

associated with the latest flush occurred at 10.4 to 11.7 weeks prior to exposure to the stress conditions (Table 6.1). The stress period varied from about 3 weeks to reach response I, about 6 weeks to reach response II and about 7 weeks to reach response III (Table 6.1). When the desired stress response was attained and the last internode started to wilt and last pair of leaves bent slightly downward in Treatment 1 and 2, leaf xylem potential (leaf WP) averaged –0.71 and –0.86 MPa, respectively (Table 6.2). Leaf xylem potentials were –0.93 and –1.08 MPa in Treatment 3 and 4, respectively, when the trees showed a greater stress response. Leaf WP of unstressed trees was –0.56 MPa, whereas the most severe water stress in Treatment 5 was –1.12 MPa (Table 6.2).

Flowering and yield responses. When the desired wilting tree response was attained and leaf WP was measured, trees were irrigated with the different 2 levels of irrigation until flowering. When flowers were observed, irrigation with 80% of daily evaporation from a class A evaporation pan was applied every 2 days to allow flowers to develop to anthesis. When stressed trees that exhibited leaf WP of –0.71 (Treatment 1) and –0.93 MPa (Treatment 3) were irrigated by additions of relatively small amounts of water (1.85-fold of daily evaporation every 3rd day) to the trees, the first flower was observed 54 days after the last rainfall, or about 31 and 8 days after the onset of irrigation, respectively (Table 6.2). Trees received a total amount of water of 202.1 and 67.3 mm/tree in Treatment 1 and 3, respectively, before flowering was observed. Mangosteen trees that were stressed to a leaf WP of –0.86 (Treatment 2) and –1.08 MPa (Treatment 4) produced the first flower 52 and 53 days after the last rainfall or about 33

and 7 days after the onset of irrigation, respectively. The total amount of water applied was 105.2 and 36.2 mm/tree. The trees, which attained the most severe stress, had leaf WP of –1.12 MPa (Treatment 5) and produced the first flower 76 days after the last rainfall or about 25 days after the onset of irrigation. Total amount of water applied was 107.4 mm/tree. The unstressed trees produced the first flower 85 days after the last rainfall with 414.5 mm/tree of water applied over 10 weeks. Although mangosteen trees were exposed to various degrees of water stress, days to full bloom (anthesis) from the appearance of the flower buds was in the same range as that of unstressed trees (30 to 34 days) (Table 6.2). After irrigation was applied to stressed trees, a lower percentage of leaf drop (7.9%) was observed on trees stressed to –0.93 MPa (Table 6.2). Leaf drop in the unstressed trees was only 1.7%. Other water-stress treatments caused between 9.3 and 10.2% defoliation. Fruit number/tree for trees that attained leaf WP of –0.93 and –1.08 MPa was significantly larger (1266.9 and 1073.4 fruit/tree, respectively) than trees exposed to greater or less severe water stress. The unstressed trees produced only 214.3 fruit/tree (Table 6.2).

6.4 Discussion

Salter and Goode (1967 cited by Tatt, 1976) suggested that water stress could be a beneficial stimulus for flowering in many tropical fruit trees. For example, floral initiation in lychee was promoted in response to a stress period (-0.9 MPa soil water potential) for 4 months (Nakata and Suehisa, 1969). A very low leaf water potential (-3.5 MPa at midday) was associated with floral induction in 2-year-old potted 'Tahiti' lime

trees (Southwick and Davenport, 1986). Similar results were described for 'Bartlett' pear, 'Shamouti' orange, and durian (*Durio zibethinus* Murr.) (Mitchell et al., 1984; Moreshet et al., 1983; Hiranpradit et al.,1991; Chandraparnik et al., 1992). A continuous dry period was crucial for flower initiation in these species, while irrigation was required to promote development of flower buds to anthesis. Nir et al. (1972) and Sale (1970) reported that in 'Eureka' lemon trees and cacao, a period of water stress initiated flower bud formation, but subsequent flower development did not proceed until the stress conditions were removed. Similarly, water stress was needed to break floral bud dormancy in coffee (Alvim, 1960), but after the dormancy was broken, irrigation or exogenous GA_3 was required to stimulate development of flower buds to anthesis (Browning, 1975; Van der Veen, 1968; Schuch et al., 1992).

Poonnachit et al. (1996) suggested that three main factors were involved in the flowering process of mangosteen. They are duration of water stress, age of apical buds, and plant vigor, which can be expressed by the following multiple linear regression model.

Percentage of flowering = 3.84 (apical bud age) + 1.87 (plant vigor)
-0.35 (drought period) –129.26 .....(6.1)

r^2 = 0.83**

where, percentage of flowering = proportion of flowering shoots to total shoots
apical bud age = age of apical buds in weeks after the emergence of the latest flush
plant vigor = degrees of vigorous vegetative growth (%)
drought period = days of exposing to continuous dry period

Once the three factors are in place, an appropriate water management is needed to trigger

flower development.

The present study supports the above flowering equation. Vigor ratings showed that trees exhibited a high degree of vigorous vegetative growth. Apical buds were at least 9-weeks-old or older following emergence of the latest flush when trees were exposed to stress conditions. Since all stressed trees produced more fruit number per tree and the number of apomictic fruit is a consequence of a corresponding number of flowers per tree, the results indicate that mangosteen flowering was stimulated by water stress. The study also indicated that after being subjected to water stress, floral buds required irrigation to emerge. After the emergence of the floral buds, 80% of daily evaporation from a class A evaporation pan was applied to stimulate normal development to anthesis.

Table 6.1 Plant vigor and age of apical buds when mangosteen trees were exposed to soil moisture stress condition.

Treatment[a] No.	Plant vigor rating	Apical bud age (weeks)		Stress period (weeks)
		at onset stress	at onset irrigation	
1	3.64	10.97	14.31	3.34
2	3.71	11.71	14.43	2.72
3	3.71	10.97	17.53	6.56
4	3.64	11.28	17.85	6.57
5	3.57	10.42	17.67	7.25
6	3.68	-	12.10	-
LSD at $P \leq 0.05$	NS	NS	7.70	0.56

[a]Treatment 1 = last internode started to wilt + 1.85-fold of total daily evaporation irrigation every 3rd day.
2 = last internode started to wilt + 35 to 40 mm/tree followed by half of that amount at 7-day-intervals.
3 = last internode noticeably wilted and last pair of leaves bent slightly downward + 1.85-fold of total daily evaporation irrigation every 3rd day.
4 = last internode noticeably wilted and last pair of leaves bent slightly downward + 35 to 40 mm/tree followed by half of that amount at 7-day-intervals.
5 = the most severely wilting symptom + 35 to 40 mm/tree followed by half of that amount at 7-day-intervals.
6 = unstressed + 1.85-fold of daily evaporation irrigation

Table 6.2 Effects of soil moisture stress and water management treatments on flowering and yield of mangosteen, Thailand.

Treatment[a]	Leaf water potential (MPa)	Irrigation before flowering (mm/tree)	Duration between onset of irrigation and appearance of flowers (days)	Days to 1st flower after the last rainfall	Flowering date	Days to full bloom	Fruit no./tree	Leaf drop after irrigation (%)
1	-0.71	202.11	30.62	54	12 Jan 98	30.29	850.48	9.29
2	-0.86	105.22	32.96	52	10 Jan 98	32.29	784.29	9.52
3	-0.93	67.30	8.08	54	12 Jan 98	32.29	1266.93	7.86
4	-1.08	36.24	7.01	53	11 Jan 98	33.71	1073.37	9.76
5	-1.12	107.43	25.25	76	2 Feb 98	34.00	753.29	10.24
6	-0.56	414.52	85	85	12 Feb 98	32.41	214.33	1.67
LSD at P < 0.05	0.07	22.32	4.59	18.24	2.38	NS	234.09	2.36

[a]Treatment 1 = last internode started to wilt + 1.85-fold of total daily evaporation irrigation every 3rd day.

2 = last internode started to wilt + 35 to 40 mm/tree followed by half of that amount at 7-day-intervals.

3 = last internode noticeably wilted and last pair of leaves bent slightly downward + 1.85-fold of total daily evaporation irrigation every 3rd day.

4 = last internode noticeably wilted and last pair of leaves bent slightly downward + 35 to 40 mm/tree followed by half of that amount at 7-day-intervals.

5 = the most severely wilting symptom + 35 to 40 mm/tree followed by half of that amount at 7-day-intervals.

6 = unstressed + 1.85-fold of daily evaporation irrigation.

An interesting point is that there appears to be an optimum degree of water stress followed by an appropriate water management regime, which stimulates more flowering. Mangosteen trees that attained leaf WP of –0.93 to –1.08 MPa received irrigation of 67.30 and 36.24 mm/tree, respectively, to promote the first flower. Trees exposed to less severe water stress (> –0.93 MPa) or more severe stress (< –1.08 MPa) received larger amount of irrigation before flowering was observed. Although trees were exposed to different stress and irrigation regimes, they produced the first flower nearly on the same day (non-significant difference at $P \leq 0.05$) but flower and fruit numbers were fewer on trees subjected to less stress than -0.93 or more stress than -1.08 MPa (Table 5.2). It appears that the degree of stress conditions and corresponding amount of irrigation affected the amount of flowering.

It has been suggested that water stress is essential to release coffee flower buds from the dormant state. Growth of the coffee flower buds that are dormant or have just been released from dormancy may be very slow because of low water uptake into buds. Increased rate of water uptake during bud development after bud dormancy is broken may be the result of increased evaporative demand by the rapidly growing flower bud and an increased amount of functional xylem elements (Astegiano et al., 1988; Schuch et al., 1994). The current study also showed that water stress as well as irrigation amount after the stress conditions was crucial for floral initiation and development in mangosteen.

Poonnachit et al. (1996) provided evidence that not only stress and plant vigor,

but also age of apical buds after the emergence of the latest flush, are essential for flowering of mangosteen. Bernier (1988) and Bernier et al. (1981) proposed that since not all shoot meristems react to conditions that promote flowering, the target meristematic cells must be competent or have the capability to respond to floral inductive conditions. Also, cells may be competent for a specific response for a limited time period. Once the meristematic cells are competent and react to inductive signal(s), then the cells become determined for a new or more restricted developmental fate (McDaniel, 1984, 1989). In mangosteen a competent apical meristem is about 9-weeks-old following the emergence of the latest flush, and a period of water stress, which is the favorable inductive condition, are the essential components for occurrence of multisequential evocational events leading to flowering.

Bernier (1988) and Bernier et al. (1981) proposed that several chemicals, assimilates and known phytohormones participate in floral induction. They also suggested that not only genetic variation but also past and present growing conditions can result in different factors becoming limiting in different species. The nutrient diversion hypothesis (Sachs and Hackett, 1983) postulates that floral induction is the result of modification of source/sink relationships within the plant in such a way that the shoot apex receives a better supply of assimilates than other plant parts. It has been suggested that water stress results in a significant increase in both leaf and xylem ABA in several plant species (Bano et al., 1993; Hubick et al., 1986; Jackson et al., 1995; Liang et al., 1997; Liang and Zhang, 1999) and a decrease in shoot cytokinins (Bano et al., 1993;

Davies and Zhang, 1991; Hubick et al., 1986; Itai and Vaadia, 1965) and root gibberellins (Hubick et al., 1986; Taylor and Railton, 1977). Therefore, water stress can cause changes in the balance of hormones which may directly affect the initiation of floral primordia, as well as the diversion of assimilates to a developing reproductive structure (Chalmers, 1985; Reid and Wample, 1985; Weaver and Johnson, 1985). Change in ABA level may alter the balance of hormones in mangosteen subjected to water stress. Floral evocation in mangosteen may be favored by a reduction in the proportion of stimulatory to inhibitory hormones. Weaver and Johnson (1985) showed that ABA often decreased sink strength, which could cause the organs that were acting as sinks to give up assimilates. Therefore, the ongoing floral evocational events in mangosteen may be supported by the mobilization of reserves from the last pair of leaves, which located next to the apical bud.

Meristems undergo evocational events until commitment of the meristem to flower becomes irreversible. This point occurs at about the time when histological and morphological changes begin and before the sign of floral initiation (Bernier, 1988; Bernier et al., 1981). The size of mangosteen apical meristem at age $\leq$ 9 weeks old, before subjected to water stress, was about 14 μm wide and 5.6 μm high. At the end of an optimum degree of stress, the meristem size increased to about 77 μm wide and 18.5 μm high and became dome shaped (S. Salakpetch and U. Poonnachit, unpublished data). Flower initiation and the early morphogenesis phase follow at the end of evocation

(Bernier et al., 1981). The present study showed that there was no appearance of flower buds until irrigation was applied, suggesting that cessation of growth of the apical buds may have occurred after the completion of evocation, flower initiation and perhaps the early morphogenesis phase. Irrigation was subsequently required to stimulate the differentiation, growth and development of apical buds. The optimum degree of water stress followed by irrigation could promote the first flower within 7 days after irrigation (Treatment 4). If the stress period was interrupted by irrigation, resulting in a lesser degree of stress, flowering was observed at a later period after the onset of irrigation. This may be because the duration of the stress was not long enough for the apical buds to rapidly progress into the flower initiation and morphogenesis phases. On the other hand, in trees subjected to the most severe stress condition (Treatment 5) all relevant processes at the shoot apex for flower induction were fully achieved and growth of the apex was arrested. Growth was resumed after water stress was alleviated by a large amount of irrigation and floral buds emerged about 25 days after the onset of irrigation. A large amount of irrigation was required to rehydrate the buds to attain the turgid state and resume normal growth and development. It is likely that the flowering process would not have proceeded further unless the stress was alleviated.

Ethylene evolution generally increases in stressed tissues or dormant buds (Abeles, 1973) and decreases when dormancy has been broken (Fuchingami and Nee, 1987; Schuch et al., 1992). Severe water stress can lead to defoliation of peach and pear trees (Proebsting and Middleton, 1980) and elevated ethylene production in stressed

plants resulted in defoliation in olive (Lang and Martin, 1987, 1989) and hydrangeas (Bailey, 1990). Thus, it is possible that ethylene promoted leaf senescence of mangosteen under stress condition, and may explain why the percentage of leaf drop after irrigation of the most severely water-stressed trees was greater when compared to the less severely water-stressed and unstressed trees. Water stress can cause changes in the balance of hormones by increasing both leaf and xylem ABA (Bano et al., 1993; Jackson et al., 1995; Liang and Zhang, 1999) and ethylene, and decreasing shoot cytokinins and root gibberellins (Bano et al., 1993; Hubick et al., 1986; Taylor and Railton, 1977) which may directly increase rate of leaf senescence (Reid and Wample, 1985) as well as decrease mobilization of assimilates to the sink organs (Chalmers, 1985; Weaver and Jackson, 1985). Therefore, the alteration of hormonal balance resulting from water stress could be another possibility to explain leaf drop on stressed trees after irrigation was applied.

It has been reported that water stress can cause the breaking of latex vessels and latex glands of mangosteen, which are found throughout the tree including branches, leaves, and flowers (S. Sadudee et al., unpublished). In the present study, when mangosteen trees were subjected to water stress, it was found that the leaf WP was not lower than –1.12 MPa although the stress period was about 11 weeks and the tree was severely wilted. This may have been due not only to osmotic adjustment to water deficit (latex solutes accumulated in the cells) but also to factors associated with cell-wall elasticity to reduce the loss of water from the cell as well as to reduce the damaging

effect of water stress (Morgan, 1984). One of the important damaging effects of water stress is the higher concentration of certain organic compounds, amino acids, and sugars, for instance, that can be toxic to cell organelles and may become inhibitory to certain enzymes and processes in the cells (Pollard and Wyn Jones, 1978; Larkam and Wyn Jones, 1979; Tyree and Jarvis, 1982). The breaking of latex vessels and latex glands at the shoot apex caused by the most severely stressed condition might have occurred and might have damaged the cells and resulted in less flowers and subsequent fruits/tree compared to that on trees subjected to the optimum degree of water stress.

This study showed that mangosteen trees subjected to an optimum level of water stress (leaf WP of – 0.93 to – 1.08 MPa) required less amounts of water to release trees from stress and to induce flowering when compared to trees exposed to less and more severe stress conditions. Although days to the first flower after the stress commenced were not significantly different among the stressed trees except for the most severely stressed trees, the appearance of the first flower bud on trees subjected to the optimum level of stress could be observed about 7 days after irrigation. Other stressed trees produced the first flower about a month after commencement of irrigation. When all factors in equation 5.1 are considered together with the results of the present study, it appears that the stress condition should be considered as *an extremely important factor*, and the optimum age of apical buds and a high degree of vigorous vegetative growth, may be *a minimum limiting factor* and *a supporting factor*, respectively, associated with floral induction, evocation, and initiation in mangosteen. Once the 3 factors are in place,

appropriate water management is crucial to promote emergence of floral buds. Also, regular irrigation was required to stimulate normal growth and development of floral buds to anthesis.

CHAPTER 7

CONCLUSION

Observations and experiments on juvenility of mangosteen have led to several conclusions regarding growth characteristics associated with the transition from the juvenile to the mature phase. In addition, information was obtained on methods to accelerate the growth of the juvenile mangosteen to attain earlier maturation and on agro-management strategies to induce flowering after the attainment of the mature phase.

The growth rates of the juvenile, near mature and mature phases were significantly different and could be used to distinguish the juvenile-to-mature transition in mangosteen. The evidence presented in this study also indicated that apart from the growth rate of the 3 different growth phases, age and canopy area were also distinct characteristics associated with the transition from the juvenile to the mature phase. The relationship between the number of flowering years and canopy area revealed that mangosteen trees attained the ability to flower when the surface area of their canopy, based on the cylindrical surface area of the trees, was about 50 m^2. Also, the first bearing in mangosteen trees began when they were 7.9 years old. When the effect of both canopy area and age on phase change were combined, it clearly indicated that canopy area was more strongly correlated with phase change than age. From these investigations, it could be concluded that phase change in mangosteen was associated with and possibly determined by the attainment of a minimum canopy size.

Photosynthetic measurement for fully mature leaves exposed to full sun of mature mangosteen trees, grown under well-managed conditions on the Chanthaburi

Horticultural Research Center research plot, showed a low value of $P_{n\,(max)}$ which may help explain the slow growth rate of mangosteen. For a more precise explanation for the slow growth rate, gas exchange characteristics of the leaves of both sun-grown juvenile and mature mangosteen trees should be determined. Information of photosynthetic characteristics and light interception could help understand the physiology of the mangosteen canopy and could be used to manipulate the canopy to maximize photosynthetic activity and in turn increase to growth and economic yield.

This study showed that the growth rate of juvenile mangosteen trees was only 0.25 meter per year when compared to trees at the near mature and the mature phase which had rates that were 0.69 and 0.49 meter per year, respectively. If the growth rate of the juvenile phase can be accelerated, mangosteen trees could transition to the near mature and mature phase more rapidly, consequently a shortened period of juvenility would result. The influences of GA_{4+7}, BA, GA_{4+7} + BA, and thiourea + dextrose as well as photoperiod were investigated to accelerate the growth of 2-year-old mangosteen trees grown under nursery conditions. All plant growth regulators were significantly effective in stimulating more flushes and increasing the number of leaves on each flush. As a consequence, mangosteen trees were taller and produced more total leaf area than the untreated trees at the conclusion of experiment. Extended daylength treatments increased leaf number on each flush, and total leaf area of juvenile mangosteen trees. At the end of this experiment, all treated trees were taller and had more total leaf area. The study showed that height of all treated trees was due to a contribution of a combination of flush number and internode elongation. Moreover, the leaf weight ratio (LWR) and leaf area ratio (LAR) were promoted by the extended days. The root weight ratio (RWR) was not

increased but was lower than the control, after a 16-month period of exposure to the extended day treatments. The enhancement of growth and total leaf area of mangosteen under nursery conditions could also be beneficial by maximizing the photosynthetically active area for tree growth and development. After field establishment, all treated trees were able to increase their canopy size more rapidly than the controls, and with this rate of growth might be able to attain the minimum size associated with phase change earlier than the control trees.

Based on the results of this study, mangosteen seedlings should be grown in a tall container with a highly fertile potting mix and under 50% shade in the nursery for 2 years. Daily irrigation with an amount of water about 75% of daily evaporation should be applied. Both soil and foliar fertilizers should also be applied regularly to maintain their normal growth. Thereafter, plant growth regulators or increasing daylength can be applied to enhance the formation of secondary branches and increase leaf area before transplanting. After field transplanting, the plant should be grown under 50% shade conditions for about a year and kept well protected from the major pests namely, thrips (*Scirtothrips* sp.), the leaf miner (*Phyllocnistis* sp. and *Melanocercops* sp.), and the leaf eating caterpillar (*Stictoptera columba*). Mangosteen trees grown under these conditions can grow and attain the minimum size as well as cumulative leaf area associated with the juvenile-to-mature transition earlier than trees grown from seedlings prepared by the traditional practices of growers. Subsequently, the first flowering can occur when trees are exposed to favorable inductive management regimes.

Water stress was demonstrated as the appropriate agro-management to induce

flowering in mangosteen. The trees produced flowers and fruited profusely when they were subjected to water stress conditions that induced leaf WP of –0.93 to –1.08 MPa followed by either 1.85 times the daily evaporation every 3rd day or by the application of 35 to 40 mm/tree only once and half of that amount at 7-day-intervals until flowering. After the floral buds emerged, mangosteen trees also required 80% of daily evaporation to stimulate normal flower development to anthesis.

The findings on growth characteristics associated with maturation of mangosteen presented in this study can be used as physiological indicators of the juvenile-to-mature transition. However, further work toward an understanding of the phase change is also required. The identification of protein marker(s) associated with phase change may provide the important information both in the further understanding of the process of phase change and in determining the favorable agro-management techniques to shorten the juvenile period of mangosteen. Another field of research that should be investigated is the role of phytohormones on phase change of mangosteen.

The present study succeeded in enhancing growth of mangosteen seedlings under nursery conditions. The potential for growth acceleration still remained after transplanting to the field. Assessment of growth and flowering should be continued to determine whether the juvenile period of mangosteen is shortened. To understand the mechanism of water stress on flowering of mangosteen more clearly, abscisic acid and carbohydrate experiments should be conducted to verify the involvement of growth regulators and carbohydrates in flowering of mangosteen.

APPENDIX A

COMPARISON OF GROWTH RATES

After logarithmic transformation, the within-phases sums of squares and products for young and near mature mangosteen trees were recorded separately, as shown on lines 1 and 2 in Table A1. Next the residual sum of squares from regression for young and near mature mangosteen was calculated and is shown on the right in lines 1 and 2. The residual mean squares, 0.0016 and 0.0015, were compared by the two-tailed F test, Hartley's test (Puri and Mullen, 1980; Snedecor and Cochran, 1980). In these data, the residual mean squares gave an F value of 1.067 with 28 and 38 degrees of freedom, giving $P < 0.05$, indicating the homogeneity of residual variances.

To compare the slopes (growth rates) or regression coefficient of young, 0.075 (0.25 in the untransformed scale), and of near mature, 0.095 (0.695 in the untransformed scale), the extended analysis of variance to obtain the F test of differences between the adjusted class mean was used (Snedecor and Cochran, 1980). In line 3 the degrees of freedom and the sums of squares of deviations from the individual regressions were added. The mean square, 0.0015, was the residual mean square when separate regression lines were fitted in each phase of growth. The pooled slope 0.089 (0.568 in the untransformed scale) and the sum of squares 0.108 which represented deviations from a regression line in which a single pooled slope was fitted, is shown in line 4. The difference, 0.108 – 0.101 = 0.007 with 1 degrees of freedom, in line 5, was the contribution of the difference between the regression coefficients of young and near mature to the sum of squares of deviations. The corresponding mean of square in line 5 was compared to the within-phases mean square, 0.0015, by the F test. In these data, $F =$

0.007/0.0015 = 4.667, degrees of freedom = 1, 66 (Table A1) confirming that the growth rates of young and near mature were different.

If further confirmation of the differences between the two regression lines was required, the y intercepts of the two lines can be compared. However, the y intercept of young and near mature mangosteen growth were negative values, -0.016 (-0.117 in the untransformed scale) and –0.096 (-2.105 in the untransformed scale), respectively, thus, it was omitted in this study. Growth rates of near mature to mature mangosteen (Fig. 2.4, line B and C), and of young to mature mangosteen (Fig. 2.4, line A and C) were compared using the same method as described above. The comparisons also showed significantly different rates of growth among those growth phases (Table A2 and A3).

Table A1 Comparison of regression lines of logarithms, growth of young and near mature mangosteen. The untransformed growth rate of young, near mature, and the pooled were 0.25, 0.695, and 0.568 meters per year, respectively.

						Deviations from regressions			*F*-value
	df	Σx^2	Σxy	Σy^2	Reg. Coeff.	df	SS	MS	
Within									
1. Young	29	20	1.503	0.157	0.075	28	0.044	0.0016	
2. Near mature	39	50	4.775	0.513	0.095	38	0.057	0.0015	*1.067*
3.						66	0.101	0.0015	
4. Pooled, W	68	70	6.277	0.671	0.089	67	0.108	0.0016	
5. Differences between slopes						1	0.007	0.007	*4.667*

Comparison of slopes: $F = 0.007/0.0015 = 4.667$ (df = 1,66) significant

Table A2 Comparison of regression lines of logarithms, growth of near mature and mature mangosteen. The untransformed growth rate of near mature, mature, and the pooled were 0.695, 0.46, and 0.444 meters per year, respectively.

						Deviations from regressions		*F*-value
	df	Σx^2	Σxy	Σy^2	Reg. Coeff.	df	SS	MS	
Within									
1. Near mature	39	50	4.775	0.513	0.095	38	0.057	0.0015	
2. Mature	49	932	27.223	0.845	0.029	48	0.050	0.0010	*1.445*
3.						86	0.107	0.0012	
4. Pooled, W	88	982	31.998	1.358	0.032	87	0.315	0.0036	
5. Differences between slopes						1	0.208	0.208	*173.33*

Comparison of slopes: $F = 0.208/0.0012 = 173.33$ (df = 1,86) significant

Table A3 Comparison of regression lines of logarithms, growth of young and mature mangosteen. The untransformed growth rate of young, mature, and the pooled were 0.25, 0.46, and 0.456 meters per year, respectively.

	df	Σx^2	Σxy	Σy^2	Reg. Coeff.	Deviations from regressions df	SS	MS	*F*-value
Within									
1. Young	29	20	1.503	0.157	0.075	28	0.044	0.0016	
2. Mature	49	932	27.223	0.845	0.029	48	0.050	0.0010	*1.541*
3.						76	0.094	0.0012	
4. Pooled, W	78	952	28.726	1.002	0.030	77	0.135	0.0017	
5. Differences between slopes						1	0.041	0.041	*33.149*

Comparison of slopes: $F = 0.041/0.0012 = 33.149$ (df = 1,76) significant

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APPENDIX B

STANDARD REGRESSION COEFFICIENT

The standard regression coefficients (Std. Reg. Coeff.) were developed to compare the strengths of the relation between different X variables on Y values in the multiple linear regression model (Snedecor and Cochran, 1980). They could be estimated as:

$$\text{Std. Reg. Coeff. } (b_{\text{canopy area}}) = [(b_{\text{canopy area}})(SD_{\text{canopy area}})] / SD_{\text{number of flowering years}}$$

Where, $b_{\text{canopy area}}$ = slope of canopy area in the multiple linear regression model

$SD_{\text{canopy area}}$ = standard deviation of canopy area data

$SD_{\text{number of flowering years}}$ = standard deviation of number of years that mangosteen flowered

Since the multiple linear regression in the present study was numbers of flowering years = 0.036(canopy area) - 0.079(age) – 0.235, $SD_{\text{canopy area}}$ and $SD_{\text{number of flowering years}}$ was 28.04 and 1.052, respectively. The standard regression coefficient of the slope of canopy area was (0.036)(28.04) / 1.052 = 0.985 and that of the slope of age was (-0.079)(1.492) / 1.052 = -0.11. This indicated that precocity of mangosteen (the first bearing) was related to its canopy area more than age.

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APPENDIX C

DETERMINATION OF PLANT VIGOR

The vigor of mangosteen trees was visually evaluated based on leaf vigor (color and size) and damages due to the major pests such as *Scirtothrips* sp. (thrips), *Phyllocnistis* sp. and *Melanocercops* sp. (leaf miner), and *Stictoptera columba* (leaf eating caterpillar). Branch health was also evaluated. The rating scales of plant vigor were:

1 = Trees exhibited very poor health. The last pair of leaves was damaged by thrips and/or leaf miner on more than 50% of total shoots. Leaves were damaged by other pests on about 30-50% of total leaf area. Branches with mechanical or pest damage were more than 50% of total branch number.

2 = Trees exhibited poor health. The last pair of leaves was damaged by thrips and/or leaf minor more than 30% but less than 50% of total shoots. Leaves were damaged by other pests about 30-50% of total leaf area. Mechanical and pest damages on branches were more than 30% of total branch number.

3 = Trees exhibited fair health. Damage from pests on leaves was more than 10% but less than 30% of total area. Mechanical and pest damages on branches were more than 10% but less than 30% of total branch number.

4 = Trees were healthy with bright color and shiny leaves. Damage from pests on leaves was about 6-10% of total area. Mechanical and/or pest damages on branches was more than 5% but less than 10% of total branch number.

5 = Trees were considerably healthy with bright color and shiny leaves. Damage from pests on leaves was less than 5% of total area. Mechanical and/or pest damages on branches was less than 5% of total branch number.

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